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Vervet monkeys greet adult males during high-risk situations

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Living in groups involves both costs and benefits. Benefits can be derived from decreased predation risk, for example due to safety in numbers, predator confusion, decreased vigilance costs, or cooperative defence (Krause & Ruxton, 2002). Costs can emerge due to competition and increased time demands for social activities, such as the maintenance of social bonds, to the detriment of other essential activities, such as foraging (Lehmann, Korstjens, & Dunbar, 2007; Majolo, de Bortoli Vizioli, & Schino, 2008). Animals thus have to balance the costs incurred from living in groups and the benefits from their interactions with other group members.

One way by which group living animals can manage their social relations is by performing ritualised behaviours during close encounters, which have been termed greetings (Hall, 1962; Brown, 1967). Greeting signals appear in various modalities, which include vocalisations (e.g. red-bellied woodpeckers, *Centurus carolinus* (Kilham, 1961), bottlenose dolphins, *Tursiops truncates* (Quick & Janik, 2012), African wild dogs, *Lycaon pictus* (Estes & Goddard, 1967), African elephants, *Loxodonta Africana*, (Poole, 2011), mantled howlers, *Alouatta palliata* (Dias, Rodriguez Luna, & Canales Espinosa, 2008) or chimpanzees, *Pan troglodytes* (Laporte & Zuberbühler, 2010)), but also facial expressions, affiliative gestures, or a variety of postures (e.g. lesser black-backed gulls, *Larus fuscus* (Brown, 1967), wild boars and warthogs, *Sus scrofa* and *Phacochoerus aethiopicus* (Frädrich, 1974), spotted hyenas, *Crocuta crocuta* (East, Hofer, & Wickler, 1993), baboons, *Papio sp.* (Smuts & Watanabe, 1990; Whitham & Maestripieri, 2003) or spider monkeys, *Ateles geoffroyi* (Aureli & Schaffner, 2007)).

Despite the fact that greeting signals are relatively widespread in group-living animals, their exact function has remained mostly unclear. The current literature suggests five main functions to explain why animals signal to each other during close range encounters. First, the ‘Benign Intent Hypothesis’ posits that individuals use greeting signals in socially tense situations (e.g. around food resources or when outcomes of interactions are unpredictable) to signal willingness to interact in a friendly way (Bauers, 1993; Silk, Cheney, & Seyfarth, 1996; Silk, 1996, 2000; Katsu, Yamada, & Nakamichi, 2014). For instance, wild female baboons use vocal signals to communicate benign intent when approaching mothers to increase the likelihood of affiliative contacts, especially with infants (Silk, Seyfarth, & Cheney, 2016).

Second, the ‘Conflict Management Hypothesis’ posits that individuals use greeting signals to avoid conflicts and repair their relationships after agonistic interactions (de Waal & Roosmalen, 1979). Reconciliatory grunts, for example, are produced by female baboons to encourage friendly approaches between former opponents (Cheney & Seyfarth, 1997). During fusion events, spider monkeys and mantled howlers also use greeting signals, such as embraces, sniffs, throat rumbles, clucks or a variety of postures, presumably as a strategy to avoid conflicts (Aureli & Schaffner, 2007; Dias et al., 2008).

Third, according to the ‘Signal Submission Hypothesis’ individuals use greeting signals to acknowledge existing dominance relationships by advertising their inferior social status, which then increases social tolerance from higher-ranking individuals (de Waal, 1986). This has been documented in wolves and dogs, *Canis lupus sp.* (Schenkel, 1967), spotted hyenas (East et al., 1993) and rhesus macaques, *Macaca mulatta* (de Waal & Luttrell, 1985). Another well-studied example is the pant-grunt of chimpanzees, produced by low-ranking individuals when encountering higher-ranking ones (Laporte & Zuberbühler, 2010).

Fourth, the ‘Social Coordination Hypothesis’ posits that individuals use greeting signals to increase group cohesion and to coordinate joint activities, which can have fitness benefits in terms of reducing predation risk (e.g. synchronised swimming of long-finned pilot whales, *Globicephala melas* (Senigaglia, de Stephanis, Verborgh, & Lusseau, 2012)) or cooperative hunting (e.g. African wild dogs (Estes & Goddard, 1967)). Similarly, male capuchins, *Cebus apella*, produce “sirena” screams to increase social coordination with allies when encountering other groups (Lynch Alfaro, 2008) and Hamadryas baboons, *Papio hamadryas*, use a ritualised form of presenting to recruit males to cooperate with them against rivals in getting access to females (Abegglen, 1984). Observations on wild chimpanzees and crested macaques, *Macaca nigra*, showed that individuals produce lip-smacks, a non-vocal but audible behaviour in which the lips moved repeatedly during face-to-face encounters, when approaching other group members to elicit affiliative interactions, such as grooming (Fedurek, Slocombe, Hartel, & Zuberbühler, 2015; Micheletta, Engelhardt, Matthews, Agil, & Waller, 2013).

Fifth, the ‘Social Bond Testing Hypothesis’ posits that individuals use greeting signals to assess the quality of their social relationships. Here, the idea is that greeting behaviour can vary in terms of completeness, reciprocity and symmetry depending on the strength of the interacting individuals’ social bond, and thus serves as a proxy to assess their mutual affiliation (Whitham & Maestripieri, 2003). Signals are often intimate or risky, such as kissing, embracing, sniffing or, for males, inspecting and touching genitals (Wang & Milton, 2003), as if males are “…literally placing their future reproductive success in the trust of another male” (Smuts & Watanabe, 1990, p.169). Generally, these kinds of greetings are often between closely bonded individuals (e.g. spotted hyenas (Smith et al., 2011), spider monkeys (Schaffner & Aureli, 2005), Tonkean macaques, *Macaca tonkeana* (De Marco, Sanna, Cozzolino, & Thierry, 2014), capuchin monkeys (Matheson, Johnson, & Feuerstein, 1996) or chimpanzees (Okamoto, Agetsuma, & Kojima, 2001)). Such potentially dangerous signals thus appear to strengthen their existing bonds.

Vervet monkeys, *Chlorocebus pygerythrus*, live in multi-male/multi-female groups and various studies on their communication system have generated insights concerning their social cognition. For example, playback experiments of screams have demonstrated that mothers distinguish their own offspring from unrelated juveniles, while bystander females can allocate juveniles to their respective mothers (Cheney & Seyfarth, 1980). Other work has shown that some call types convey relatively specific meanings to recipients, as demonstrated by the monkeys' reactions to playbacks of predator-specific alarm calls (Seyfarth, Cheney, & Marler, 1980; but see Price et al., 2015) and playbacks of different grunt variants (Cheney & Seyfarth, 1982).

Grunts are an acoustically heterogeneous soft call type, produced in a range of situations, which includes group progression, as well as intra- and intergroup encounters (Struhsaker, 1967). During intragroup encounters, grunts appear to function as a greeting signal, and it has been proposed that the calls signal submission and inhibit aggressive behaviours from higher-ranking group members (Struhsaker, 1967). Although vervet monkeys have been studied extensively, we are not aware of any systematic research on greeting behaviour. During pilot observations, we noted that adults often produced grunts while approaching males near rivers, where predation risk is high (see Appendix A1). Therefore, we generated a new functional hypothesis, the 'Risk Reduction Hypothesis', which posits that greeting signals are produced in dangerous situations to group members who are most valuable in situations of danger (Krause & Ruxton, 2002). In vervet monkeys, adult males are most vigilant and play the most active role in predation defence (Baldellou & Henzi, 1992), but individuals should also greet closely bonded individuals who are also likely to provide support in risky situations (e.g. macaques (Berghänel, Ostner, Schröder, & Schülke, 2011; Micheletta et al., 2012) or dwarf mongooses, *Helogale parvula* (Kern & Radford, 2016)).

The goal of our study was to describe the general patterns of greeting behaviours of wild vervet monkeys and examine the function of vocal signals produced in this context. To this end, we first examined individual, dyadic and ecological factors that triggered grunts during close encounters in an intra-group context. Specifically, we investigated the influence of sex, relative rank difference and strength of social bonds between interacting partners, as well as the influence of visibility (habitat type) and predation risk (i.e. close to rivers, high risk areas where most natural predator encounters occur in our study site; Appendix 1).

Following this analysis, we used multi-model inference to explore the function of grunts produced during dyadic encounters in male vervet monkeys. We identified five predictor variables to test the six hypotheses outlined before. Two predictors described the social relationship between the interacting individuals, i.e. relative rank differences ('Signal Submission Hypothesis') and social bonds strength ('Social Bond Testing Hypothesis'). Two further predictors described the ecological situation when signalling occurred. First, close to rivers may require coordinating movement ('Social Coordination Hypothesis') and support by valuable group members, i.e. adult males ('Risk Reduction Hypothesis'), since predation risk is high near rivers (Appendix 1). Another predictor was the presence of contestable food ('Conflict Management Hypothesis') which is likely to increase aggression (Isbell, 1991). A final predictor described whether calls were given by the approaching individual ('Benign Intent Hypothesis'), to signal its willingness for a peaceful interaction.

We used an information-theory approach to compare a set of six competing, non-exclusive models, representing the six described functional hypotheses of greeting behaviour in animals (Table 1, Table 4; Appendix 4). This approach allowed us to compare and rank our models in terms of how well they fit the existing data (Burnham & Anderson, 2003; Burnham, Anderson, & Huyvaert, 2011). Information-theory is a viable alternative to more traditional falsification-based hypothesis testing with *P*-values. Its advantage is that it produces insights into the relative importance of the different hypotheses, which are represented by different combinations of biologically relevant predictors (i.e. statistical models) that, in our case, may govern vervet monkey greeting behaviour. We created six models using combinations of the predictors and their interaction terms where appropriate to address the six hypotheses, such that each model represented one hypothesis (Table 1).

TABLE 1

METHODS

Ethical Note

Our study was approved by the relevant local authority, Ezemvelo KZN Wildlife, and by the University of Cape Town, South Africa. The study conforms with the ASAB/ASB guidelines for the Treatment of Animals in Behavioural Research and Teaching (ASAB, 2012). We used non-invasive methods of data collection to observe animals in their natural habitats, and all individuals were habituated to human observers. We identified all individuals based on physical characteristics, such as body size and shape, scars and/or broken digits.

Study site and species

We studied individuals in five wild groups of vervet monkeys over a year (13 March 2014 – 17 March 2015) in the Mawana Game Reserve in KwaZulu-Natal, South Africa (S28°00.327; E031°12.348). Mawana is a 12’000-hectare private game reserve situated in a Savannah biome. Group size in our groups varied from four to over 56 individuals and their home range sizes approximated 160 hectares (van de Waal, Borgeaud, & Whiten, 2013). Most of the groups contained multiple adult males and females with many juveniles. Group composition varied between groups and over time due to birth, death and migratory events (Table 2). We considered males as adult (AM) after their first migration while females were considered as adult (AF) after they had given birth for the first time.

TABLE 2

Behavioural definitions

We defined an encounter as an approach between a focal animal and a partner within five meters. An encounter ended whenever one of the participants moved beyond this distance. During those close encounters, individuals could interact in friendly or aggressive ways, or not interact at all. Since the vocalisations produced by the focal animal during those meetings were short-distance soft calls of low frequency with a guttural acoustic quality, we classified them as grunts, although they occasionally graded into higher-pitched signals of longer duration (Struhsaker, 1967, see Appendix 5). Since we examined social encounters during dyadic interactions, no other monkeys were present in the 5m surrounding the two participants, thus allowing us to infer the receiver of the calls thanks to body orientation and/or gazing behaviour of the signaller. We defined vocal encounters as dyadic interactions during which the focal produced at least one grunt, in contrast to silent encounters during which no call was produced.

Data Collection

General

We collected focal animal data (Altmann, 1974) from 23 well-habituated individuals (12AF & 11AM) belonging to three out of the five study groups (BD, IN & NH; Table 2) over 8 months (9 May 2014 – 3 January 2015, total = 206 h of focal data collected between 5:15am until 5:30pm, mean = 9.0, range = 6.1-19.0). During focal follows, we collected dyadic encounter data on an all-occurrence basis, specifying whether greeting signals have been produced or not. For each encounter, we also collected whether it occurred close to rivers (GPS data) and the habitat type (satellite imagery by Google Earth v7.1.5.1557; 8 July 2016; https://www.google.com/earth/). Relevant social information, such as the identity of all individuals present within 10m of the focal animal were also collected using instantaneous sampling every 15 minutes (see Appendix 2; Altmann, 1974). We considered two data points as independent if one of the partners changed, or if two consecutive encounters with the same participants were separated by at least 10 minutes.

Function

Although vervet monkeys sometime produce non-vocal signals, such as body presentations, lip-smacks or various postures during close encounters, we focused on the most obvious signals produced during dyadic interactions, the grunts. Here, we defined the caller as the individual producing a vocal signal while facing and/or looking at another specific individual, the receiver. We focused on the greeting behaviour of adult males because females rarely produced grunts and because their calls were often barely audible. In addition to collect dyadic encounter data between males within 5m, we also recorded all-occurrence data of such vocal interactions between two males in four out of five study groups (AK, BD, KB & NH; Table 2) between 13 March 2014 and 17 March 2015 (Appendix 2). Although we might have missed some vocal encounters, we are confident that our data reflect the general patterns of male greeting behaviour.

Inter-Observer Reliability

We insured inter-observer reliability by first completing an identification test, during which each observer had to correctly recognise all individuals three times in a row within 30s. Second, we calculated inter-observer reliability on instantaneous samples on the focal animal collected simultaneously by two observers (i.e. main activity, height, distance to refuge, position in group, group spread, distance to nearest neighbour and the number of neighbours in 10m). We considered our behavioural data to be collected reliably if the proportions of agreement observed between two observers were significantly different from the ones expected by chance (Cohen's Kappa, SM-MC: $k = 0.63$, $P < 0.001$, N = 79; SM-EC: $k = 0.58$, $P < 0.001$, N = 60; SM-JMdB: $k = 0.81$, $P < 0.001$, N = 60; (Cohen, 1960)). Although we had somewhat low Cohen's Kappa values they are still considered fair if ranging from 0.4 to 0.6 and good if between 0.6 and 0.8 (Watkins & Pacheco, 2000).

Dominance status

We determined dominance ranks of adults based on the outcomes of dyadic agonistic interactions collected *ad libitum* and during focal animal sampling using Elo-rating (Neumann et al., 2011). By continuously updating each individual's rating after each conflict, Elo-ratings of individuals allow monitoring dominance status over time by reflecting the competitive abilities of each individual while taking into account the social dynamics of a group during a desired timescale. We defined losers of dyadic dominance interactions as those individuals ending the interaction by showing submissive behaviours and/or retreating, while the other individuals were defined as winners. From individual Elo-ratings, we calculated pairwise differences for all dyads. We standardized Elo-ratings of each dyad according to three sex combinations (male/male, female/female, female/male), thus allowing comparisons of standardized differences of each dyad type (see Appendix 3). Although absolute differences could help us understanding the influence of the social rank of a specific individual on its greeting behaviour (e.g. investigating whether grunts are produced by low vs. high-ranking individuals), we used relative differences between two individuals as we were interested to examine the influence of small vs. large real rank differences between two participants on their vocal greetings. Ratings were calculated with k = 100 (Neumann et al., 2011), using the 'EloRating' package version 0.43 (Neumann & Kulik, 2014).

Social Bonds

To quantify the strength of social bond between pairs of individuals we calculated the Dyadic Composite Sociality Index (DSI; Appendix 3; Silk, Cheney, & Seyfarth, 2013). This index, based on the Composite Sociality Index (Sapolsky, Alberts, & Altmann, 1997), generates a score reflecting the strength of dyadic affiliative relationships. For its calculation, we used three social behaviours: grooming bouts per observation time (continuously sampled during focal follows), nearest neighbour (i.e. the closest individual of the focal based on instantaneous samples collected every 15 minutes) and proximity (i.e. all individuals within 10m of the focal animal based on instantaneous samples collected every 15 minutes). The average DSI value across all dyads in a given group by definition equals one. Larger values indicated stronger than average bonds and values between zero and one indicate lower than average bonds (Silk et al., 2013). Calculations were carried out using the 'socialindices' package version 0.46-7 (Neumann, unpublished).

Statistical Analyses

General

We used focal data to describe the general greeting behaviour of vervet monkeys, i.e. which focal animals vocalised towards which partners. We analysed 308 clear dyadic interactions between all adults, involving 23 focal individuals (12AF & 11AM) and 46 partners (28AF & 18AM). We used a generalized linear mixed model (GLMM, Baayen, Davidson, & Bates, 2008) fitted with a binomial structure and logit-link function. We used the vocal behaviour of the focal animal as a response variable, i.e. whether it produced a grunt or not (Yes=1/No=0). We added six predictor variables describing the individuals involved, the relationship between them, and the ecological situation in which an encounter occurred (Table 3; see Appendix 4).

TABLE 3

In addition to the six fixed effects, we included both the identity of the focal animal and its partner as random intercepts to control for repeated measurements. After checking for collinearity between variables using variance inflation factors (maximum VIF = 1.1), we calculated Cook's distances to look for influential individuals (Nieuwenhuis, te Grotenhuis, & Pelzer, 2012). We identified five potentially influential individuals that accounted for a total of 49 encounters during which no greeting signals were produced (one female and two males as focal individuals; two female partners). However, their removal resulted in only minor changes in parameter estimates, which did not affect our conclusions, so we present results on our full data set. Moreover, although graphical analyses of residuals (using half-normal plots) revealed one observation as an outlier, we decided not to remove it, as it concerned an adult male grunting towards the second highest-ranking female, while all other greeting signals were produced towards adult males. In conclusion, although we are aware of the high variation in our model, caused by influential individuals, we decided to run and interpret it to obtain first insights into a rare but socially important behaviour, vocal greeting in wild vervet monkeys.

Function

We used behavioural data during adult male dyadic vocal encounters to examine the functions of grunts. To this end, we built one specific model for each of the six hypotheses, which included a combination of the five predictors, plus their interaction terms when necessary (Table 4).

(1) For the 'Benign Intent Hypothesis', we included the presence of food as a predictor variable as it increases the risk of social tension (Isbell, 1991). This was because, in other work, we had noticed that providing rich food dramatically increased aggression rates in our groups (van de Waal, personal observations). Thus, we expected more grunts around valuable food. We also included the initiator calling, i.e. whether the individual actively approaching was grunting or not, as we expected initiators to call more frequently to show their peaceful intention (Bauers, 1993). Finally, we added the interaction term between both predictors since initiators should be more interested in reducing tension during feeding.

(2) For the 'Conflict Management Hypothesis', we included rank difference as a predictor variable as conflicts are more likely to escalate between males of similar rank (Smith & Parker, 1976), between which we expected more greeting signals. Consequently, we used a quadratic term in this model as we expected grunting to be common if rank differences were close to zero, but not if rank differences were very negative or very positive. We also included the strength of social relationship between the two participants, as it is more important to repair relationships after conflicts with valuable partners. This has already been demonstrated by reconciliation rates in chimpanzees, which are higher between philopatric males who form strong alliances, than between females who have weaker bonds (de Waal, 1986). We thus expected closely bonded individuals to produce more greetings to strengthen their valuable relationships. Finally, we included the presence of food as a predictor variable, as we expected grunt production to increase in these socially tense situations to reduce the risk of aggression.

(3) For the 'Signal Submission Hypothesis', we included rank difference as a predictor variable as acknowledging existing dominance relationships should increase social tolerance (de Waal, 1986). We expected more greetings between animals of similar dominance status as it might be advantageous for those individuals to avoid ambiguities, and thus to reduce the risk of conflict escalation (Smith & Parker, 1976). We also included the presence of food in this model, as social ranks influence access to food, with dominants often monopolizing valuable items (e.g. red deer stags, *Cervus elaphus* (Appleby, 1980), rainbow trout, *Salmo gairdneri* (Metcalfe, 1986), and vervet monkeys (Whitten, 1983)). Consequently, we expected greetings to be especially important in the presence of food, when competition was high.

(4) For the ‘Social Coordination Hypothesis’, we included two social and two ecological variables. First, we included rank difference in the model mainly because, in vervet monkeys, higher-ranking individuals are more likely to initiate group progressions (Baldellou, 1991) and should therefore produce more greetings. Second, we included social bond strength as a predictor variable because closely bonded partners are more likely to benefit from close proximity (Senigaglia et al., 2012) and should produce more calls than individuals with weaker bonds. Third, we included the presence of food, as increased grunt production during feeding may help to optimise spacing and minimise competition (Gros-Louis, 2004). Finally, we added close to rivers as a fourth predictor variable, as grunts should increase social cohesion in high predation areas (Appendix 1; Krause & Ruxton, 2002). We thus expected an increased calling rate near rivers. In addition to these four main predictors, we also added interaction terms that appeared meaningful to us (Table 4). We expected all individuals to call in risky situations (presence of food or predators) to benefit from decreased risks. However, we expected higher-ranking individuals, playing central roles as group leaders, to produce more greetings in peaceful environments (absence of valuable resources and low predation risk), or while moving into open areas, to enhance social cohesion and synchronise activities, as lower-ranking individuals were more likely to follow their movement (Cheney & Seyfarth, 1992). Similarly, despite all individuals benefitting from increased fitness by remaining in close proximity to closely bonded partners, we expected higher-ranking individuals to produce more greetings when interacting with non-friends to incite them to synchronise activity. Finally, we expected closely bonded individuals to produce more greetings in peaceful situations, i.e. in the absence of food and predators.

(5) For the 'Social Bond Testing Hypothesis', we included social bond strength and the presence of food as predictor variables, since closely bonded partners should produce more greetings than individuals with weaker bonds (Whitham & Maestripieri, 2003). Since the presence of food increases the risk of aggression (Isbell, 1991), we expected increased call production around food resources, as social bond testing might be especially important in these socially tense situations.

(6) For the 'Risk Reduction Hypothesis', we included social bond strength as support from bystanders, such as cooperative defence against potentially dangerous males or predators, increases with bond strength (Berghänel et al., 2011; Micheletta et al., 2012). Individuals with strong bonds should produce more greeting signals. We also included initiator calling as a predictor variable, as initiating an interaction in dangerous situations help decreasing predation risks by increasing vigilance (Brown, 1999). We thus expected individuals approaching partners (initiators) to call more frequently than individuals being approached. As in our study area, most predator encounters occurred near rivers (Appendix 1), we finally added close to rivers as a last predictor variable. Individuals should increase grunt production mainly in these dangerous areas to attract individuals and benefit from group-related anti-predator effects (Krause & Ruxton, 2002).

TABLE 4

After removing incomplete data (missing identity of one or both participant(s), for example due to unfavourable observation conditions), we analysed 53 vocal encounters in 25 dyads. Our modelling strategy here focused on whether or not we observed a greeting signal in any given dyad under different conditions. Similar to Kulik et al (2012), we restructured our data set to include each dyad (N = 58 possible dyads) once in each of our different combinations of predictor variables (resulting in N = 752 data points; see Appendix 4 for details on the methods used to restructure the initial dataset). To account for repeated data for each dyad introduced by this procedure, we added dyad identity as random intercept in each model, in addition to caller identity, receiver identity and group identity. We then scored for each of these possibilities whether or not we actually observed a greeting (Yes=1/No=0), which served as the response variable in the models. Hence, our models assessed under which conditions greetings were more likely to occur and thus be observed.

We used Akaike's Information Criterion corrected for small sample size (AICc; Burnham et al., 2011) to rank our models according to how likely they were given our data (for an example of study using similar methods see e.g. (Duboscq, Romano, Sueur, & MacIntosh, 2016)). We considered the model having the smallest AICc value as the one explaining best our observations, with all other models having an increasing AICc score having relative weaker explanatory value. One of the principles of AICc (and similar information criteria, Grueber, Nakagawa, Laws, & Jamieson, 2011) is that it represents a trade-off between model fit and complexity. Better fit is invariably achieved by increasing the number of predictors in a model, but comes at the cost of increasing complexity. However, AICc includes a "penalty" term that increases the value of AICc if more predictors are added to a model (Anderson, 2008). Given two models with the same fit but with different numbers of predictors, the AICc will be smaller for the model with the smaller number of predictors, i.e. for the same fit, the less complex model will be ranked better.

Inference from such model comparisons can be drawn in multiple ways. First, differences in AICc values between two models can be used to assess plausibility of the lower-ranked model. For example, models with ΔAICc values larger than about 15 will be dismissed by most as implausible compared to the higher-ranked model (Anderson, 2008). Despite this, Anderson (2008, p.85) explicitly advises against using ΔAICc values for creating artificial cut-off points. More intuitively, standardized model weights express the probability that a given model is the best among those in the set of models tested (Anderson, 2008) and thus allow for a more gradual examination of evidence for or against specific models. As a cautionary note, it has to be mentioned that any comparison of multiple models in this framework is relative, not absolute, i.e. if a model is identified as the best model, this model is the relative best one in the candidate set (Anderson, 2008). Possible models that were not included in the candidate set might be better still (i.e. with smaller AICc) than the best model in the candidate set.

For each model, we used generalized linear mixed models (GLMM; Baayen et al., 2008) fitted with a binomial structure and logit-link function. We used whether or not we actually observed a greeting signal within a dyad as the response variable, but for ease of discussion, we will refer to it as whether one individual produced at least one grunt (Yes=1/No=0). We entered caller and receiver identity, as well as dyad as random intercepts to control for repeated measurements. We also added group identity as a random intercept to avoid bias due to group size and composition. Predictor variables and their interactions differed between models (Table 1; Table 4; Appendix 4). Model assumptions (maximum VIF = 1.0, homogeneity of residuals using half-normal plots and Cook's distances) were tested on a full model including all the five predictors. Since all assumptions were satisfied without any influential cases, we considered all simpler models to be suitable for analysis (Slobodeanu, personal communication).

All tests were performed using R v3.3.1 (Team, 2016) with the glmer function, lme4 package v1.1.11 (Bates, Mächler, Bolker, & Walker, 2015) and the MuMIn package v1.15.6 (Barton, 2016).

RESULTS

Grunts produced during close social encounters are a rare behaviour in wild vervet monkeys produced in only 20 out of 384 dyadic interactions (5.2%) during 206h of focal follows (Fig 1; mean call rate = 0.1 per hour, mean duration of encounter = 4.30 min, range = 0.03 – 66.00 min; Appendix 2).

FIGURE 1

General

We analysed N=308 complete observations of dyadic encounters to examine the general pattern of vervet monkeys greeting behaviour (Table 5). A likelihood ratio test revealed a significant difference between the full and null models ($\chi^2_6 = 15.67$, $P = 0.016$), suggesting that our full model was more informative than the corresponding null model.

TABLE 5

Although both males and females vocalised, grunts were almost exclusively produced towards adult males (95%) with all but one vocalisations being produced towards males (Table 5; Fig 2; exception of one male greeting a high-ranking female). There was no influence of the sex of the focal, the social relationship between participants (rank difference and social bond strength) and habitat visibility. However, grunts tended to be more likely to occur near rivers (Fig 1; 12% of encounters occurring near rivers were vocal whereas vervet monkeys produced grunts in 4% of encounters away from rivers).

FIGURE 2

Function

We analysed a dataset of 53 vocal dyadic encounters between adult males collected during both focal and *ad libitum* samplings (Appendix 2). The model comparison is summarised in Table 6 and detailed model results are presented in Appendix 4.

TABLE 6

Comparison of model weights and AICc differences between the six models indicated highest support for the 'Risk Reduction Hypothesis' and the 'Benign Intent Hypothesis' (Table 6). The risk reduction model, including the whether the initiator called, strength of social bonds and close to rivers as variables, had the highest model probability (0.90) of being the best model among the six we compared. The second best model in our set, the benign intent model, which includes the presence of food and whether the initiator called as predictors, had a model probability of 0.10 (ΔAICc = 4.3). The remaining four models (i.e. signal submission ΔAICc = 21.2, social bond testing ΔAICc = 22.0, conflict management ΔAICc = 22.2 and social coordination ΔAICc = 26.6 models) had a combined probability of less than 0.01. These results suggest that vervet monkey greeting signals most likely serve to reduce risks by communicating to other individuals in dangerous areas, such as near rivers, and to a lesser extent, grunts might also be used to signal benign intent.

DISCUSSION

Although a rare behaviour produced only in 5.2% of dyadic encounters, both male and female vervet monkeys produced vocal signals when approaching other group members. However, with one exception, only interactions involving males' partner triggered those vocalisations. Results from the analysis of focal data of close dyadic encounters (Table 5; Appendix 2) suggested little to no influence of the social relationship between participants, indicating that greeting signals were produced between individuals independently of their rank difference or social bond strength. Despite results on the influence of ecological variables not being statistically significant, vervet monkeys tended to greet each other more often near rivers, where predation risk was high (Fig 1; Appendix 1).

One possibility to explain the rarity of vervet monkey grunts is that individuals may use other, non-vocal signals for the same purpose, which might differ between the sexes. For example, to establish friendly relationships, females may perform other behaviours, such as socially targeting grooming (van de Waal, Spinelli, Bshary, Ros, & Noë, 2013) or infant handling (Fruteau, van de Waal, van Damme, & Noë, 2011). Since males have less stable dominance relationships than females, which have to be re-established after each migration event (Cheney & Seyfarth, 1992), they may have evolved additional mechanisms to deal with this challenge. During social interactions, subordinates vervet monkeys produce grunts as part of "Red, White and Blue" displays, i.e. a dominant individual exposes his red peri-anus, white medial pelage stripes and blue scrotum to a subordinate, who responds with a submissive posture and grunting (Struhsaker, 1967). This visually based ritualised display used during close dyadic encounters, appears to help males in acknowledging dominance relations, as they are performed by dominants in front of subordinates who responded by crouching and vocalising. The behavioural difference between males and females might thus explain why males exchanged most of the greeting signals. However, visual signals might be less useful in risky areas where predator attacks occur rapidly and unexpectedly. In these circumstances, it seems more beneficial to interact vocally, especially if signals function to recruit others to anti-predator behaviour in low visibility areas, such as riverine forests. Acoustically inconspicuous grunts may be especially useful in these situations, as they minimise the risk of being detected by predators.

Overall, our data most strongly supported the ‘Risk Reduction Hypothesis’ and, to a lesser degree, the ‘Benign Intent Hypothesis’. The former suggests that vervet monkeys should call preferentially while approaching socially important partners when predation risk is high (i.e. near rivers; Appendix 1), while the latter suggests that calling might be used by initiators to mitigate social interactions during socially tense situations, such as near valuable food resources. We found only little support for the four remaining hypotheses, suggesting that, unlike chimpanzees (Laporte & Zuberbühler, 2010), vervet monkeys from our studied groups do not use greeting signals to acknowledge dominance, nor as a conflict management tool, as shown in baboons (Colmenares, 1991a, 1991b). Also, vervet monkeys do not seem to grunt to reinforce social relationships, as shown in male Tonkean macaques (De Marco et al., 2014) and finally grunts do not appear to increase social cohesiveness, coordinate activity or promote cooperation between group members, as shown in African wild dogs (Estes & Goddard, 1967).

Results from the general analysis are also in line with the ‘Risk Reduction Hypothesis’ (including three predictor variables: initiator calling, close to rivers and social bond strength), indicating that calls function to recruit valuable partners during danger to reduce predation risks since grunts were preferentially produced to adult males (Table 5). Adult males usually lead in group progressions, and the alpha male plays an essential role in these initiations (Baldellou, 1991). During risky river crossings, adult and sub-adult males are usually both at the front and back of the group (Bodin, 2015). Moreover, males are more vigilant and more active during predator encounters than females (Baldellou & Henzi, 1992). Following Hamilton's model of the selfish herd (Hamilton, 1971), this suggest that more vulnerable individuals, being in a central position, benefit from increased protection thanks to the ideal location of those peripheral males. The enhanced rates of grunts directed mainly towards adult males might be the result of callers seeking to encourage males to occupy these important spatial positions. However, future studies investigating the behaviour of receivers will be necessary to further validate the risk reduction hypothesis. In particular, the prediction is that support to signallers increases after grunt production during close encounters in situation of danger, for example by deterring predators or forming coalitions to repel potential rival males.

Second, although not significant, we found grunt production more likely when two individuals encountered each other near rivers (Fig 1; Table 5). Wild vervet monkeys often cluster as a cohesive group before crossing rivers (SM personal observations). Individuals arriving early at crossing locations wait for other group members to arrive and this is likely to cause social tension among them, which in turn might increase their calling rate. Vervet monkeys might thus produce greeting signals to reduce risks of injuries by increasing tolerance and reducing conflicts before river crossing. Results from a recent study showed that wild female baboons produce grunts to signal peaceful interactions, especially when encountering unpredictable partners (Silk et al., 2016). Similarly to spider monkeys that use embraces to reduce aggression risk during fusion events (Aureli & Schaffner, 2007), vervet monkeys might use greeting signals to reduce social risks due to agonistic interactions during socially tense situations, such as while waiting before crossing rivers.

Third, despite results from the general analysis showing little to no influence of strength of the social relationship between the two interacting individuals on grunt production in our studied groups, we included social bond strength as another predictor variable of our risk reduction model. Social bonds generally enhance cooperation between individuals (Berghänel et al., 2011), and it has been shown, for instance in male baboons, that closely bonded partners produce more greetings than other individuals having weaker bonds (Whitham & Maestripieri, 2003). In addition to increase social coordination with allies, as male capuchins do when encountering other groups for example (Lynch Alfaro, 2008), greeting signals in vervet monkeys might help maintaining social bonds, which is likely to be of special importance in risky situations, such as near rivers (Micheletta et al., 2012; Kern & Radford, 2016).

Our study has several limitations. First, although we used a 10m distance during the pilot study to define an encounter, reducing it to a distance of 5m helped improving the quality of the data due to better visibility and more reliable identification of individuals. However, individuals sometimes gave greeting signals over much greater distances, so the reported call rates are most likely underestimates. For the all-occurrence data, we only focused on vocal encounters (without distance criterion) but we had to exclude many of them because of identification problems due to low visibility or a lack of clarity about whom the signaller was trying to address.

Second, multi-model inference relies on the validity of the models compared (Anderson, 2008; Burnham et al., 2011). The approach ranks models relative to each other. It is possible that we overlooked a relevant hypothesis or misspecified models such that they did not address the hypotheses properly. Regardless of these pitfalls, we are convinced that the advantages of multi-model inference outweigh these potential drawbacks. Future studies can build upon the models we presented here and refine them if necessary to allow further insights into the functions of greeting calls in particular, and signals more generally.

Often close social interactions involve a range of signals, sometimes a mixture of vocal and non-vocal ones. Greetings have been well documented in baboons as they use sequential combinations of different patterns (facial, vocal, postural, manipulatory and locomotory) to assess their relationships, and thus negotiate their status without fighting (Colmenares, 1990). For instance, baboons can use facial displays, such as ear-flattening or grimaces to signal willingness to interact in a friendly way, while simultaneously accompany some of their greetings by vocalisations uttered by one or both participants (Colmenares, 1991a, 1991b). Several species of macaques also use combinatorial signals. For example, facial displays such as lip-smacking, are combined with different vocalisations when engaging in positive social interactions (Partan, 2002; De Marco, Cozzolino, Dessì-Fulgheri, & Thierry, 2011; Micheletta et al., 2013). In chimpanzees, 74% of pant-grunts are produced in conjunction with other communicative signals, such as facial expressions or gestures, directed at specific individuals (Taglialatela et al., 2015). However, each participant might use specific signals. Wolves and dogs for example, use different signals according to their social rank. While the alpha individual produce vocal signals when approaching the pack, subordinates greet with several forms of submissive postures, such as lying on the back or “nose-push” gestures (Schenkel, 1967).

Although vervet monkeys use multi-modal signals when encountering each other, for example by combining grunts with “Red, White and Blue” displays (Struhsaker, 1967), we only focused on the vocal channel, mainly because the frequency of social encounters involving only two individuals within 5m being was low. Nonetheless, animals might communicate flexibly by using different signals in specific contexts to convey different messages. For instance, “contest hoots” produced by bonobos, *Pan paniscus*, to challenge males, are used in combination with different type of gestures, which provide extra cues on the forthcoming social interaction. In this species, soft gestures were more likely to be produced during friendly plays, whereas rough ones often preceded agonistic interactions (Genty, Clay, Hobaiter, & Zuberbühler, 2014). Consequently, future studies should focus on multi-modal signals to deepen our understanding of the complexity of such social rituals.

Another way a signaller can gain flexibility during communication is to use the same signal for different functions, and our findings may be an example. For example, it is possible that during close encounters subjects mainly signalled benign intent to potentially aggressive males, while over greater distances the same calls might function to increase vigilance from others. Another example of the multi-functionality of a signal is the use of different forms of ritualised greetings in Hamadryas baboons, to signal submission, avoid conflicts and form alliances (Fraser & Plowman, 2007). Similarly, spotted hyenas also use greetings for two main purposes, i.e. to reinforce social bonds and to effectively communicate cooperative affiliations (Smith et al., 2011). Further detailed investigations on this vocal signal, including acoustic analysis, multi-modal signalling as well as contextual variations, might reveal additional functions than the use of greetings by vervet monkeys to recruit individuals in dangerous situations and to signal willingness to interact in friendly ways.

Data Availability

We archived our data and code in a publicly available repository (Mercier et al., 2017; https://figshare.com/s/259509e0b8b29fe81b90, doi:10.6084/m9.figshare.4203339), following best practices (White et al., 2013; Roche, Kruuk, Lanfear, & Binning, 2015).

REFERENCES

Abegglen, J.-J. (1984). *On socialization in hamadryas baboons: a field study*. Bucknell University Press: Associated University Presses, Cranbury, N. J.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*(3), 227-266.

Anderson, D. R. (2008). Information Theory and Entropy. *Model Based Inference in the Life Sciences: A Primer on Evidence* (pp. 51-82): Springer New York.

Appleby, M. C. (1980). Social rank and food access in red deer stags. *Behaviour, 74*(3), 294-309.

ASAB. (2012). Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour, 83*(1), 301-309. doi:https://doi.org/10.1016/j.anbehav.2011.10.031

Aureli, F., & Schaffner, C. M. (2007). Aggression and conflict management at fusion in spider monkeys. *Biology Letters, 3*(2), 147-149.

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of memory and language, 59*(4), 390-412.

Baldellou. (1991). *Implications of the multi-male troop structure in vervet monkeys (Cercopithecus aethiops pygerythrus).* (PhD Thesis), University of Natal, South Africa.

Baldellou, & Henzi, S. P. (1992). Vigilance, predator detection and the presence of supernumerary males in vervet monkey troops. *Animal Behaviour, 43*(3), 451-461.

Barton, K. (2016). MuMIn: Multi-Model Inference. R package version 1.10. 0. 2014. Retrieved from http://cran.r-project.org/package=MuMIn

Bates, D. M., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4. *Journal of Statistical Software, 67(1)*, 1-48. doi:10.18637/jss.v067.i01

Bauers, K. A. (1993). A functional analysis of staccato grunt vocalizations in the stumptailed macaque (Macaca arctoides). *Ethology, 94*(2), 147-161.

Berghänel, A., Ostner, J., Schröder, U., & Schülke, O. (2011). Social bonds predict future cooperation in male Barbary macaques, Macaca sylvanus. *Animal Behaviour, 81*(6), 1109-1116.

Bodin, M. (2015). *Socio-spatial organisation of a wild Vervet monkeys (Chlorocebus aethiops) population during risky area crossings.* (Master thesis), University of Strasbourg & University of Neuchâtel, Unpublished.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol, 24*(3), 127-135.

Brown. (1967). Courtship behaviour in the Lesser Black-backed Gull, Larus fuscus. *Behaviour, 29*(2), 122-152.

Brown. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary Ecology Research, 1*(1), 49-71.

Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: a practical information-theoretic approach*: Springer Science & Business Media.

Burnham, K. P., Anderson, D. R., & Huyvaert, K. P. (2011). AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral Ecology and Sociobiology, 65*(1), 23-35.

Cheney, D. L., & Seyfarth, R. M. (1980). Vocal recognition in free-ranging vervet monkeys. *Animal Behaviour, 28*(2), 362-367.

Cheney, D. L., & Seyfarth, R. M. (1982). How vervet monkeys perceive their grunts: field playback experiments. *Animal Behaviour, 30*(3), 739-751.

Cheney, D. L., & Seyfarth, R. M. (1992). *How monkeys see the world: Inside the mind of another species*: University of Chicago Press.

Cheney, D. L., & Seyfarth, R. M. (1997). Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Animal Behaviour, 54*(2), 409-418.

Cohen, J. (1960). A coefficient of agreement for nominal scales. *Educational and psychological measurement, 20*(1), 37-46.

Colmenares, F. (1990). Greeting behaviour in male baboons, I: communication, reciprocity and symmetry. *Behaviour, 113*(1), 81-115.

Colmenares, F. (1991a). Greeting behaviour between male baboons: oestrous females, rivalry and negotiation. *Animal Behaviour, 41*(1), 49-60.

Colmenares, F. (1991b). Greeting, aggression, and coalitions between male baboons: demographic correlates. *Primates, 32*(4), 453-463.

De Marco, A., Cozzolino, R., Dessì-Fulgheri, F., & Thierry, B. (2011). Collective arousal when reuniting after temporary separation in Tonkean macaques. *American Journal of Physical Anthropology, 146*(3), 457-464.

De Marco, A., Sanna, A., Cozzolino, R., & Thierry, B. (2014). The function of greetings in male Tonkean macaques. *American Journal of Primatology, 76*(10), 989-998.

de Waal, F. B. M. (1986). The integration of dominance and social bonding in primates. *The Quarterly Review of Biology*, 459-479.

de Waal, F. B. M., & Luttrell, L. M. (1985). The formal hierarchy of rhesus macaques: an investigation of the bared-teeth display. *American Journal of Primatology, 9*(2), 73-85.

de Waal, F. B. M., & Roosmalen, A. (1979). Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology, 5*(1), 55-66.

Dias, P. A., Rodriguez Luna, E., & Canales Espinosa, D. (2008). The functions of the" Greeting Ceremony" among male mantled howlers (Alouatta palliata) on Agaltepec Island, Mexico. *American Journal of Primatology, 70*(7), 621.

Duboscq, J., Romano, V., Sueur, C., & MacIntosh, A. J. J. (2016). Scratch that itch: revisiting links between self-directed behaviour and parasitological, social and environmental factors in a free-ranging primate. *Royal Society Open Science, 3*(11). doi:10.1098/rsos.160571

East, M. L., Hofer, H., & Wickler, W. (1993). The erect 'penis' is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. *Behavioral Ecology and Sociobiology, 33*(6), 355-370.

Estes, R. D., & Goddard, J. (1967). Prey selection and hunting behavior of the African wild dog. *The Journal of Wildlife Management*, 52-70.

Fedurek, P., Slocombe, K. E., Hartel, J. A., & Zuberbühler, K. (2015). Chimpanzee lip-smacking facilitates cooperative behaviour. *Scientific reports, 5*.

Frädrich, H. (1974). A comparison of behaviour in the Suidae. *The behaviour of ungulates and its relation to management, 1*, 133-143.

Fraser, Ó., & Plowman, A. B. (2007). Function of notification in Papio hamadryas. *International Journal of Primatology, 28*(6), 1439-1448.

Fruteau, C., van de Waal, E., van Damme, E., & Noë, R. (2011). Infant access and handling in sooty mangabeys and vervet monkeys. *Animal Behaviour, 81*(1), 153-161.

Genty, E., Clay, Z., Hobaiter, C., & Zuberbühler, K. (2014). Multi-modal use of a socially directed call in bonobos. *Plos One, 9*(1), e84738.

Genty, E., Neumann, C., & Zuberbühler, K. (2015). Complex patterns of signalling to convey different social goals of sex in bonobos, Pan paniscus. *Scientific reports, 5*.

Gros-Louis, J. (2004). The function of food-associated calls in white-faced capuchin monkeys, Cebus capucinus, from the perspective of the signaller. *Animal Behaviour, 67*(3), 431-440.

Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: challenges and solutions. *Journal of evolutionary biology, 24*(4), 699-711.

Hall, K. R. L. (1962). The sexual, agonistic and derived social behaviour patterns of the wild chacma baboon, Papio ursinus. *Journal of Zoology, 139*(2), 283-327.

Hamilton, W. D. (1971). Geometry for the selfish herd. *Journal of theoretical Biology, 31*(2), 295-311.

Isbell, L. A. (1991). Contest and scramble competition: patterns of female aggression and ranging behavior among primates. *Behavioral Ecology, 2*(2), 143-155.

Katsu, N., Yamada, K., & Nakamichi, M. (2014). Development in the Usage and Comprehension of Greeting Calls in a Free-Ranging Group of Japanese Macaques (Macaca fuscata). *Ethology, 120*(10), 1024-1034.

Kern, J. M., & Radford, A. N. (2016). Social-bond strength influences vocally mediated recruitment to mobbing. *Biology Letters, 12*(11), 20160648.

Kilham, L. (1961). Reproductive behavior of Red-bellied Woodpeckers. *The Wilson Bulletin*, 237-254.

Krause, J., & Ruxton, G. D. (2002). *Living in groups*: Oxford University Press.

Kulik, L., Muniz, L., Mundry, R., & Widdig, A. (2012). Patterns of interventions and the effect of coalitions and sociality on male fitness. *Molecular Ecology, 21*(3), 699-714.

Laporte, M. N. C., & Zuberbühler, K. (2010). Vocal greeting behaviour in wild chimpanzee females. *Animal Behaviour, 80*(3), 467-473.

Lehmann, J., Korstjens, A. H., & Dunbar, R. I. M. (2007). Group size, grooming and social cohesion in primates. *Animal Behaviour, 74*(6), 1617-1629.

Lynch Alfaro, J. (2008). Scream–embrace displays in wild black-horned capuchin monkeys. *American Journal of Primatology, 70*(6), 551-559.

Majolo, B., de Bortoli Vizioli, A., & Schino, G. (2008). Costs and benefits of group living in primates: group size effects on behaviour and demography. *Animal Behaviour, 76*(4), 1235-1247.

Matheson, M. D., Johnson, J. S., & Feuerstein, J. (1996). Male reunion displays in tufted capuchin monkeys (Cebus apella). *American Journal of Primatology, 40*(2), 183-188.

Mercier, S., Neumann, C., Van de Waal, E., Chollet, E., Meric de Bellefon, J., & Zuberbuhler, K. (2017). *Data and supplementary material for: Vervet monkeys greet adult males during high-risk situations*. Retrieved from: https://figshare.com/s/259509e0b8b29fe81b90

Metcalfe, N. B. (1986). Intraspecific variation in competitive ability and food intake in salmonids: consequences for energy budgets and growth rates. *Journal of Fish Biology, 28*(5), 525-531.

Micheletta, Engelhardt, Matthews, Agil, & Waller. (2013). Multicomponent and multimodal lipsmacking in crested macaques (Macaca nigra). *American Journal of Primatology, 75*(7), 763-773.

Micheletta, Waller, B. M., Panggur, M. R., Neumann, C., Duboscq, J., Agil, M., & Engelhardt, A. (2012). Social bonds affect anti-predator behaviour in a tolerant species of macaque, Macaca nigra. *Proceedings of The Royal Society B,* pp. 4042-4050.

Micheletta, J., Engelhardt, A., Matthews, L., Agil, M., & Waller, B. M. (2013). Multicomponent and multimodal lipsmacking in crested macaques (Macaca nigra). *American Journal of Primatology, 75*(7), 763-773.

Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., . . . Engelhardt, A. (2011). Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Animal Behaviour, 82*(4), 911-921.

Neumann, C., & Kulik, L. (2014). EloRating: Animal Dominance Hierarchies by Elo Rating. R package version 0.43. Retrieved from http://cran.r-project.org/package=EloRating

Nieuwenhuis, R., te Grotenhuis, H. F., & Pelzer, B. J. s. (2012). influence.ME: Tools for Detecting Influential Data in Mixed Effects Models. *R Journal, 4*(2), 38-47.

Okamoto, K., Agetsuma, N., & Kojima, S. (2001). Greeting behavior during party encounters in captive chimpanzees. *Primates, 42*(2), 161-165.

Partan, S. R. (2002). Single and multichannel signal composition: facial expressions and vocalizations of rhesus macaques (Macaca mulatta). *Behaviour, 139*(8), 993-1027.

Poole, J. H. (2011). Behavioral contexts of elephant acoustic communication. In C. J. Moss, H. Croze, & P. C. Lee (Eds.), *The Amboseli elephants: a long-term perspective on a long-lived mammal.* (pp. 125-161): The University of Chicago.

Price, T., Wadewitz, P., Cheney, D. L., Seyfarth, R., Hammerschmidt, K., & Fischer, J. (2015). Vervets revisited: A quantitative analysis of alarm call structure and context specificity. *Scientific reports, 5*.

Quick, N. J., & Janik, V. M. (2012). Bottlenose dolphins exchange signature whistles when meeting at sea. *Proceedings of the Royal Society of London B: Biological Sciences*, rspb20112537.

Roche, D. G., Kruuk, L. E. B., Lanfear, R., & Binning, S. A. (2015). Public data archiving in ecology and evolution: how well are we doing? *PLoS Biol, 13*(11), e1002295.

Sapolsky, R. M., Alberts, S. C., & Altmann, J. (1997). Hypercortisolism associated with social subordinance or social isolation among wild baboons. *Archives of General Psychiatry, 54*(12), 1137-1143.

Schaffner, C. M., & Aureli, F. (2005). Embraces and grooming in captive spider monkeys. *International Journal of Primatology, 26*(5), 1093-1106.

Schenkel, R. (1967). Submission: its features and function in the wolf and dog. *American Zoologist, 7*(2), 319-329.

Senigaglia, V., de Stephanis, R., Verborgh, P., & Lusseau, D. (2012). The role of synchronized swimming as affiliative and anti-predatory behavior in long-finned pilot whales. *Behavioural processes, 91*(1), 8-14.

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Monkey Responses to Three Different Alarm Calls: Evidence of Predator Classification and Semantic Communication. *Science, 210*(4471), 801-803.

Silk, J. B. (1996). Why do primates reconcile? *Evolutionary Anthropology Issues News and Reviews, 5*(2), 39-42.

Silk, J. B. (2000). The function of peaceful post-conflict interactions: an alternate view. In F. Aureli & F. B. M. de Waal (Eds.), *Natural Conflict Resolution* (pp. 179-181): Univiversity of California Press, Berkeley, CA.

Silk, J. B., Altmann, J., & Alberts, S. C. (2006). Social relationships among adult female baboons (Papio cynocephalus) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology, 61*(2), 183-195.

Silk, J. B., Cheney, D. L., & Seyfarth, R. M. (1996). The form and function of post-conflict interactions between female baboons. *Animal Behaviour, 52*(2), 259-268.

Silk, J. B., Cheney, D. L., & Seyfarth, R. M. (2013). A practical guide to the study of social relationships. *Evolutionary Anthropology: Issues, News, and Reviews, 22*(5), 213-225.

Silk, J. B., Seyfarth, R. M., & Cheney, D. L. (2016). Strategic Use of Affiliative Vocalizations by Wild Female Baboons. *Plos One, 11*(10), e0163978.

Smith, & Parker, G. A. (1976). The logic of asymmetric contests. *Animal Behaviour, 24*(1), 159-175.

Smith, Powning, K. S., Dawes, S. E., Estrada, J. R., Hopper, A. L., Piotrowski, S. L., & Holekamp, K. E. (2011). Greetings promote cooperation and reinforce social bonds among spotted hyaenas. *Animal Behaviour, 81*(2), 401-415.

Smuts, B. B., & Watanabe, J. M. (1990). Social relationships and ritualized greetings in adult male baboons (Papio cynocephalus anubis). *International Journal of Primatology, 11*(2), 147-172.

Struhsaker, T. T. (1967). Auditory communication among vervet monkeys (Cercopithecus aethiops). In S. A. Altmann (Ed.), *Social communication among primates* (pp. 281-324): University of Chicago Press.

Taglialatela, J. P., Russell, J. L., Pope, S. M., Morton, T., Bogart, S., Reamer, L. A., . . . Hopkins, W. D. (2015). Multimodal communication in chimpanzees. *American Journal of Primatology, 77*(11), 1143-1148.

Team, R. C. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2015. Retrieved from https://www.r-project.org/

van de Waal, E., Borgeaud, C., & Whiten, A. (2013). Potent social learning and conformity shape a wild primate's foraging decisions. *Science, 340*(6131), 483-485.

van de Waal, E., Spinelli, M., Bshary, R., Ros, A. F. H., & Noë, R. (2013). Negotiations over grooming in wild vervet monkeys (Chlorocebus pygerythrus). *International Journal of Primatology, 34*(6), 1153-1171.

Wang, E., & Milton, K. (2003). Intragroup social relationships of male Alouatta palliata on Barro Colorado Island, Republic of Panama. *International Journal of Primatology, 24*(6), 1227-1243.

Watkins, M. W., & Pacheco, M. (2000). Interobserver agreement in behavioral research: Importance and calculation. *Journal of behavioral education, 10*(4), 205-212.

White, E. P., Baldridge, E., Brym, Z. T., Locey, K. J., McGlinn, D. J., & Supp, S. R. (2013). Nine simple ways to make it easier to (re) use your data. *Ideas in Ecology and Evolution, 6*(2).

Whitham, J. C., & Maestripieri, D. (2003). Primate rituals: the function of greetings between male Guinea baboons. *Ethology, 109*(10), 847-859.

Whitten, P. L. (1983). Diet and dominance among female vervet monkeys (Cercopithecus aethiops). *American Journal of Primatology, 5*(2), 139-159.

APPENDIXES

APPENDIX 1. PREDATOR ENCOUNTER ANALYSIS

We used *ad libitum* data on all predator encounters collected between 18 February 2013 until 30 January 2016 by trained researchers to investigate the spatial distribution of predator encounters. We used GPS data from 172 predator encounters collected on seven groups (AK, BD, CR, IN, KB, LT, NH) for which the predator had been seen and the species identified. We divided predators into three main categories (Seyfarth et al., 1980) and considered the following species: snakes (boomslang, *Dispholidus typus*, Mozambique spitting cobra, *Naja mossambica*, black mamba, *Dendroaspis polylepis*, puff adder, *Bitis arietans*, and python, *Python natalensis*), eagles (Martial eagle, *Polemaetus bellicosus*, Tawny eagle, *Aquila rapax*, African hawk eagle, *Aquila spilogaster*, and brown snake eagle, *Circaetus cinereus*), and mammals (black-backed jackal, *Canis mesomelas*, caracal, *Caracal caracal*, and serval, *Leptailurus serval*). We considered predator encounters to be near rivers if they were within 100m from the riverbed using satellite imagery (by Google Earth v7.1.5.1557; 8 February 2014; https://www.google.com/earth/, Table A1; Fig. A1).

TABLE A1

Although vervet monkeys encountered all predator types, encounters with snakes (34%) and eagles (46%) were more frequent than encounters with mammalian predators (20% including jackals 19%, caracals 0.5%, and servals 0.5%; Pearson's Chi-squared test: $X^2_2 = 8.58$, $P = 0.014$). The field site is part of a private reserve used for hunting and the population of carnivores is managed in order to maintain sufficient game for hunting. Both eagles and snakes were encountered more frequently near rivers than terrestrial mammals, which appeared to be more common away from rivers (Table A1, Fig. A2; 3-sample test for equality of proportions without continuity correction: $X^2_2 = 10.28$, $P = 0.006$). Consequently, we considered areas near rivers being dangerous as they corresponded to areas in which encounters with the more common predator types were more frequent.

FIGURE A1

FIGURE A2

APPENDIX 2. OBSERVATIONAL DATA

TABLE A2

TABLE A3

TABLE A4

TABLE A5

APPENDIX 3. FRIENDSHIP AND DOMINANCE

i) Friendship

We used the Dyadic Composite Sociality Index (DSI) to assess the social bond strength of dyads (c.f. Silk et al., 2013; see also Silk, Altmann, & Alberts, 2006). We calculated the DSI of each dyad of focal individuals by using the frequency of three social behaviours of focal animals over the study period: grooming bouts per observation time (continuously sampled during focal follows), nearest neighbour (i.e. closest individual of the focal based on instantaneous samples collected every 15 minutes) and proximity (i.e. all individuals present within 10m of the focal animal based on instantaneous samples collected every 15 minutes). These data allowed us to quantify strength of social bonds between two individuals using the following equation from Silk et al. (2013):

$$DSI_{xy} = \frac{\frac{Gxy}{G} + \frac{Pxy}{P} + \frac{Nxy}{N}}{3}$$

Here, $\frac{Gxy}{G}$ corresponds to the number of grooming bouts in which the dyad xy participated divided by the mean number of grooming bouts for all dyads in the group G. $\frac{Pxy}{P}$ corresponds to the number of instantaneous samples in which xy were in proximity of each other (i.e. within 10m) and one of them was the focal individual divided by the mean number of instantaneous samples of proximity for all dyads involved in the study P. And $\frac{Nxy}{N}$ corresponds to the number of instantaneous samples in which xy were nearest neighbours of each other (i.e. closest individuals) and one of them was the focal individual divided by the mean number of instantaneous samples of nearest neighbours for all dyads involved in the study N. The rates of the three behaviours were corrected for the observation time and co-residency of dyads. The average DSI value across all dyads in a given group by definition equals one. Larger values indicated stronger than average bonds and values between zero and one indicate lower than average bonds (Silk et al., 2013). Calculations were carried out using the "socialindices" package (version 0.46-07, Neumann et al, unpublished).

As the calculation of the DSI included grooming, a non-aggressive physical contact used to maintain social relationships (van de Waal, Spinelli, et al., 2013), it limits our possibilities to disentangle between two functional hypotheses that could operate for the "Social Bond Testing Hypothesis": individuals use greetings to establish social bonds or individuals greet because they share strong bonds. Although it is an interesting topic for future studies, we unfortunately do not have the data enabling us to disentangle these two hypotheses. However, we do not think that this is a major issue as we were interested in the more general prediction of the Social Bond Testing Hypothesis, which is that vervet monkeys use greeting signals to strengthen their social bonds.

ii) Dominance

We used *ad libitum* dyadic agonistic interactions between adults in order to establish the dominance hierarchy of vervet monkeys using Elo-rating (Neumann et al., 2011). For each observed dyadic dominance interaction, we defined the loser as the individual ending the interaction by showing submissive behaviours and/or retreating (Table A6), while the other individual was defined as winner. Only complete data were included in the analyses, i.e. when the identities of both individuals were known and their winner/loser status could be assigned without ambiguity. At least one winner and/or loser's behaviour presented in Table A6 had to occur during an agonistic interaction to define the winner/loser status of both individuals with certitude, despite some other behaviours might have been produced by one or both opponents (for example approaching, looking for support or screaming).

TABLE A6

Since we were interested in examining the effects of dominance status difference between two individuals rather than individual dominance status, we defined three dyad types according to the sex of the dyad members: male-male, female-female, and mixed dyads including interactions between all adults (male-female and female-male). We then extracted Elo-ratings of each dyad member for each day of data collection (see Fig A3). We standardized their Elo-ratings within each dyad type by scaling the Elo-rating differences between the focal and the partner to a mean of zero and a standard deviation of one. Doing so allowed us comparisons of standardized differences of each dyad type (i.e. a difference of 100 is similar across the three dyad types when comparing the social rank difference of pure male, pure female or of heterosexual interactions). Ratings were calculated with k = 100 (Neumann et al., 2011), using the EloRating package version 0.43 (Neumann & Kulik, 2014).

FIGURE A3

APPENDIX 4. STATISTICAL ANALYSES

I) General Analysis

Although 384 encounters were collected during focal follows, we only analysed 308 encounters (19.8% incomplete data removed) involving 23 well-habituated individuals (12AF & 11AM) belonging to three out of five studied groups (BD, IN & NH) over 8 months (9 May 2014 – 3 January 2015). We excluded 101 observations that were collected on juveniles because we did not collect data to establish their dominance status or friendships.

We built a generalized linear mixed model fitted by maximum likelihood using Laplace approximation (Bolker et al., 2009) with a binomial error structure and logit link function ("glmer" provided by the package "lme4"; Bates et al., 2015). We used this model to describe the general greeting behaviour of vervet monkeys, i.e. under which condition greetings were produced. Whether or not the focal individual produced a grunt during an encounter served as a response variable in our model. We introduced six variables in order to check the influence of both individual characteristics (focal and partner sex), characteristics of the relationship between the two interacting individuals (standardised rank difference and DSI reflecting social bonds strength), and two relevant ecological factors (close to rivers and habitat type). We included both the identity of the focal and of the partner as random intercepts to control for repeated measurements. We transformed numerical explanatory variables when necessary to approximate symmetric distributions of our predictor variables (i.e. we log-transformed DSI).

II) Function Analysis

We focused on the greeting behaviour of adult males because females rarely produced grunts and because their calls were often barely audible. Here, we defined the caller as the individual producing a vocal signal and the receiver as the individual responding to it. In addition to collect dyadic encounter data between males within 5m, we also recorded all-occurrence data of such vocal interactions between two males in four out of five study groups (AK, BD, KB & NH; Table 2) between 13 March 2014 and 17 March 2015 (Appendix 2). We collected 891 dyadic interactions, from which we excluded 338 observations involving females and juveniles (Focal data excluded: 229AF, 9JuvF, 28JuvM; Partner data excluded: 28AF, 14JuvF, 30JuvM) and 14 observations from LT group as no social data were collected on this group (meaning we could not calculate rank difference and social bond strength). We excluded further 96 observations for which we could not identify at least one of the participants and 89 observations during which we were not confident on the identity of the caller (our study focused on calls produced by the focal only). We also removed data from unhabituated males (defined by the number of days present in the study group prior to data collection, and whether or not the male has been seen in other habituated groups previously) to avoid observation bias as habituated males were more likely to be observed than shyer ones remaining at the periphery. We excluded 27 observations from nine unhabituated males from three groups (one in AK, five in BD and three in NH). As we wanted to investigate the function of greeting signals, we kept only male-male dyadic interactions during which grunts were produced, thus excluding 243 observations were no vocal signals have been produced and five encounters during which other calls than grunts were produced (mostly aggression calls).

As a result, we analysed greetings occurring between 25 male dyads. Since some individuals were more vocally active than other group members, some dyads were observed greeting more often than others (mean = 3.16 vocal encounters per dyad, range = 1 – 18). Consequently, we transformed the response variable into a binomial structure, i.e. whether or not a greeting signal was produced at least once in a given situation in a specific dyad (Table A7).

TABLE A7

Our modelling strategy here focused on whether or not we observed a greeting signal in any given dyad under different conditions. We used Kulik and colleagues' approach (Kulik et al., 2012) to create an expanded table (see Table A8; see also Genty, Neumann, and Zuberbühler (2015) for another example). We first selected all the males that were present at least one day in our studied groups as potential subjects. We then created a table including all dyads that could potentially have interacted with each other, given they were co-resident in the same group at one point. However, we took care to remove all self-dyads, as well as unhabituated males. Since both males from any dyad could have been either the caller or the receiver, we represented the dyad twice in our table, thus already doubling the amount of data. We then assumed that encounters of each dyad could potentially occur in all combinations of our conditions. In other words, we expanded our data table containing all the observations we could have made using all the dyads in all conditions. For instance, by including the categorical variable "Close to rivers", we again doubled the size of the data set as we assumed that encounters of each dyad could have happened either close to rivers (Yes=1), or away from them (No=0). Consequently, by adding two more categorical variables, "Caller approached" (Yes=1/No=0) and "Feeding involved" (Yes=1/No=0), we multiplied the amount of data by four. We then added information on the social relationship between the two males involved in the dyad, i.e. their rank difference as well as their social bond strength. Finally, we added the response variable: whether a grunt has actually been observed in a dyad at least once or not (Yes=1/No=0), thus again doubling the amount of data. With this method, each dyad (N=58 possible dyads) in which a greeting could have been potentially observed, was represented multiple times according to different combinations of predictor variables. However, each dyad was represented only once for each specific condition, such as for example “Close to rivers = Yes”, “Caller approached = Yes” and “Feeding involved = No”. Moreover, in addition to the identity of both males, we also included group and dyad as random intercepts in all our models to avoid pseudo-replication. As a result, we analysed a restructured dataset with 752 data points that represent the conditions under which a greeting could have potentially occurred, from which we actually observed 53 (about 7%), i.e. we observed a male producing a grunt towards another male under specific circumstances. In addition to investigate what individuals do, examining under which conditions individuals do not do it, also helps us understanding the functional aspects of this behaviour.

TABLE A8

The following table A9 is an excerpt from our data set and illustrates this approach. It depicts a specific dyad (Art/Lek). Art was the caller and Lek the receiver in the first half of the table, whereas their roles were reversed in the second part of the table. Three further combinations are depicted: close to rivers (i.e. within 100m of the riverbed), caller approached (i.e. whether the caller was the individual actively approaching the partner) and feeding context (i.e. whether some feeding behaviour was involved). In this example, we observed one greeting between Art/Lek that took place away from rivers (Close to rivers = No), where Art who was the caller, approached (Caller approached = Yes) and during which no feeding was involved (Feeding involved = No, see line 3 in table A9). In contrast, we did not observe a greeting between Art/Lek as we never observed Art greeting in a feeding context while approaching Lek close to rivers (line 2 in table A9). In contrast to Art who we observed producing a grunt in only one condition out of the eight possible ones, we observed Lek greeting Art under five specific circumstances out of the eight possible (lines 10, 12, 13, 14, 16 in table A9).

TABLE A9

TABLE A10

TABLE A11

TABLE A12

TABLE A13

TABLE A14

TABLE A15

APPENDIX 5. ACOUSTIC

We recorded all vocalisations produced by the focal animal, its partner or any neighbouring individuals opportunistically during the study period using a Marantz digital recorder PMD661 (sampling rate of 44.1 kHz, resolution 24 bits) and a Sennheiser unidirectional microphone MKH416. Recordings were then transferred to a computer and spectrograms were extracted using a Fast Fourier Transformation (time steps = 1000, frequency steps = 500, Gaussian window shape, window length = 0.05ms and dynamic range = 70dB) in PRAAT 5.4.13 (www.praat.org). We classified a vocalisation as grunt if it was produced by an individual while another identified group member was approaching or being approached by the signaller. These calls of short duration had a guttural acoustic quality, and were either produced once or several times in sequences (Fig A4, see wav files in supplemental material for example of grunts produced by a male and a female towards an adult male; (Struhsaker, 1967)).

FIGURE A4

TABLES

Table 1. Descriptive summary of the six tested hypotheses

Hypothesis	Description	References
Benign Intent	Promote friendly interactions and increase social tolerance	(Bauers, 1993; Silk et al., 2016; Silk, 2000; Katsu et al., 2014; Silk, 1996)
Conflict Management	Mitigate agonistic interactions and repair social relationships after conflicts	(de Waal & Roosmalen, 1979; Cheney & Seyfarth, 1997; Colmenares, 1990; Aureli & Schaffner, 2007; Dias et al., 2008)
Signal Submission	Acknowledge existing dominance relationships, reduce aggression and increase group stability	(Laporte & Zuberbühler, 2010; East et al., 1993; Schenkel, 1967; de Waal, 1986; de Waal & Luttrell, 1985)
Social Coordination	Increase group cohesion, coordinate joint activities and benefit from anti-predatory group effect	(Estes & Goddard, 1967; Abegglen, 1984; Lynch Alfaro, 2008; Senigaglia et al., 2012; J. Micheletta, A. Engelhardt, L. Matthews, M. Agil, & B. M. Waller, 2013; Fedurek et al., 2015)
Social Bond Testing	Assess relationships quality, strengthen social bonds and increase support from closely bonded individuals	(Whitham & Maestripieri, 2003; Wang & Milton, 2003; Smuts & Watanabe, 1990; Smith et al., 2011; Schaffner & Aureli, 2005; De Marco et al., 2014; Matheson et al., 1996; Okamoto et al., 2001)
Risk Reduction	Recruit valuable individuals during risky situations and reduce both aggression and predation risks	(Baldellou & Henzi, 1992; Berghänel et al., 2011; Kern & Radford, 2016; Micheletta et al., 2012)*

* Although we suggested this new 'Risk Reduction Hypothesis', we used references here to highlight the importance of valuable partners, such as adult males and closely bonded individuals, during risky situations.

Table 2. Group composition of the groups at the beginning and end of the study period.

	AM		AF		Group Size		Analyses	
Group	2014	2015	2014	2015	2014	2015	*General*	*Function*
AK	3	4	9	10	33	42	-	X
BD	3	9 (7)	7	12 (5)	45	56 (12)	X	X
IN	1	1	3	3 (2)	4	5 (2)	X	-
KB	3	1	4	5	24	21	-	X
NH	4	7 (4)	10	12 (5)	48	53 (9)	X	X

AM and AF correspond to the number of adult males and females respectively and group size corresponds to the total number of individuals present within each group, including juveniles, in March 2014 & 2015. Numbers in brackets correspond to the number of focal animals used in each group in March 2015. We added a cross in the last two columns to represent the groups we used for each analysis as we used focal data from three groups to analyse the general pattern of vervet monkey greeting behaviour while we used all-occurrence data from four groups to investigate the functions of grunts.

Table 3. Description of the predictors used to examine the general pattern of greeting signals

Predictors	**Description**	**Scale**
Sex focal	Sex of the focal individual	Categorical (Male/Female)
Sex partner	Sex of the partner participating in the dyadic encounter with the focal	Categorical (Male/Female)
Elo-rating difference	Relative Elo-rating difference between the two participants, a bigger difference indicating a larger difference	Numerical (Standardized across dyad type)
Social bond strength (DSI)	Score describing the strength of the social bond between the two participants, a bigger score indicating a stronger relationship	Numerical (Log-transformed)
Close to rivers	Whether the encounter occurred close to rivers, i.e. within 100m of riverbed	Categorical (Yes/No)
Habitat closed	Whether the encounter occurred in a closed habitat, defined by a vegetation cover >75%	Categorical (Yes/No)

Table 4. Description of the five predictors used to examine the potential functions of grunts

Predictors	**Rank difference**	**Social bond strength (DSI)**	**Presence of food**	**Initiator calling**	**Close to rivers**
Description	Relative Elo-rating difference between participants, bigger values indicating larger difference	Strength of relationship between two participants, bigger scores indicating stronger relationships	Whether at least one of the partner was feeding	Whether the individual approaching (initiating the interaction) produced a greeting call	Whether the encounter occurred close to rivers (within 100m of riverbed)
Scale	Numerical	Numerical (Log-transformed)	Categorical (Yes/No)	Categorical (Yes/No)	Categorical (Yes/No)
Benign Intent			X[1]	X[1]	
Conflict Management	X*	X	X		
Signal Submission	X		X		
Social Coordination	X[1, 2, 3]	X[1, 4, 5]	X[2, 4]		X[3, 5]
Social Bond Testing		X	X		
Risk Reduction		X		X	X

* We used a quadratic term for rank difference in the conflict management model (see text "(2) Conflict Management Hypothesis" for details). Identical superscripts for the benign intent and the social coordination models indicate interaction terms.

Table 5. Results of the GLMM testing social and ecological factors affecting grunt production

	Estimate	SE	*Z*	CI *	*P*
Intercept	-8.28	2.02	-4.09	-12.24 to -4.31	4.27e-05
Sex focal (Male)	0.84	0.95	0.89	-1.02 to 2.71	0.376
Sex partner (Male)	3.80	1.36	2.79	1.13 to 6.47	0.005
Elo-rating difference	0.01	0.42	0.03	-0.82 to 0.84	0.977
Social bond strength (DSI)	-0.23	0.41	-0.57	-1.03 to 0.57	0.570
Close to rivers (Yes)	1.15	0.69	1.66	-0.21 to 2.50	0.097
Habitat closed (Yes)	0.64	0.89	0.73	-1.10 to 2.38	0.468

* CI = 95% confidence intervals using Wald method, test levels of categorical predictor are given in parentheses.

Table 6. Results of multi-model inference

Models	K	AICc	ΔAICc	Weight
Risk Reduction	3	292.3	--	0.896
Benign Intent	3	296.6	4.3	0.104
Signal Submission	2	313.4	21.2	0.000
Social Bond Testing	2	314.3	22.0	0.000
Conflict Management	3	314.4	22.2	0.000
Social Coordination	9	318.9	26.6	0.000

The six models represent the six hypotheses about the functions of vervet monkey greeting signals. We sorted models by their AICc scores. K = number of terms included; AICc = Akaike's Information Criterion corrected for small sample size; ΔAICc= difference in AICc scores between the model with the lowest AICc and the following one; weight = model probabilities

Table A1. Distribution of predators encounters according to their proximity to rivers (N=172)

Close to rivers	Eagle	Mammal	Snake
Yes	50	12	38
No	28	23	21
Total encounters	78	35	59

Table A2. Data collected during instantaneous sampling of our focal animals every 15 minutes

Date	Date of the day
Group	Identity of the group in which the focal individual belongs to
Focal individual	Identity of the focal individual
Nearest adult neighbour	Identity of the nearest adult neighbour of the focal individual
Nearest juvenile neighbour	Identity of the nearest juvenile neighbour of the focal individual For mothers, infant were not recorded as nearest neighbour unless no other juvenile neighbours were present within 10m
# + ID neighbours in 10m	Number and identities of all the neighbours present within 10m of the focal animal
Remarks	Anything of interest (e.g. if target individual was crossing the river at the time of sampling)

Table A3. Observation time and number of encounters collected on each focal from three groups

Group	Focal identity	Sex	Observation time (h)	Numbers of encounters
BD	Ouli	Female	7.52	16
BD	Asis	Female	10.72	25
BD	Mooi	Female	6.55	14
BD	Numb	Female	7.50	14
BD	Riss	Female	8.43	20
BD	Oku	Male	7.65	20
BD	Lek	Male	10.68	28
BD	Ham	Male	7.47	31
BD	Neu	Male	6.25	20
BD	Zur	Male	8.85	28
BD	Tor	Male	9.17	23
BD	Che	Male	7.90	15
IN	Wiet	Female	7.83	16
IN	Bemi	Female	11.55	16
NH	Pari	Female	7.5	9
NH	Pret	Female	7.42	1
NH	Upps	Female	10.73	2
NH	Xaix	Female	7.75	16
NH	Bogo	Female	6.12	11
NH	Can	Male	8.25	17
NH	Ert	Male	19.08	13
NH	Gov	Male	13.00	14
NH	LSk	Male	8.5	15
		Female	99.62	160
TOTAL		Male	106.82	224
		All	**206.47**	**384**

Table A4. Data collected during an encounter between two individuals, i.e. an approach within 5m

Date	Date of the day
Group	Identity of the group in which the focal individual belongs to
GPS location	GPS location of the focal individual when an encounter occurred
Focal individual	Identity of the focal individual
ID partner	Identity of the partner, i.e. individual approaching or being approached within 5m of the focal individual
Approaching individual	Identity of who is approaching the other one, i.e. who initiate the encounter (*Focal, Partner, Both or Unknown*)
# + ID Neighbours in 10m	Number and identities of all the neighbours present within 10m of the focal animal
Vocalisation Produced	Whether vocalisations were produced or not
- **ID caller**	Identity of the caller
- **Type**	Type of vocalisation produced (*e.g. grunts, aggressive calls, screams…*)
- **Duration**	Duration of the first vocalisation produced in seconds (*<10s, 11-30s, 31-60s, >60s, Unknown*)
- **Resume calling**	Whether the caller resume calling after 5 seconds of silence (*Yes/No*)
- **Vocalisation rec**	Whether the vocalisations were recorded or not (*Yes/No*)
- **Track number**	Number of track on which the vocalisations were recorded on
Other signals produced	Whether other non-vocal signals were produced (*Yes/No*)
What signal?	Description of any other signal produced *(e.g. lip-smacking or submissive postures)*
Interaction	Whether the type of interaction between both individuals was *Neutral* (if there was no interaction), *Affiliative* (if they entered in contact in a friendly way, i.e. sitting in contact or grooming) and *Agonistic* (if some aggressive behaviours were produced by either individuals, such as stare, attack or chase)
Description	Ad libitum description of what happened during the encounter and any other interesting facts

Table A5. Encounter rate and grunt production of all focal individuals that produced at least one signal.

Focal identity	**Group**	**Sex**	**Elo-ratings**	**Encounter rate (per hour)**	**Grunt production (per hour)**	**Partner identities (Age/Sex class; Elo-ratings)**
Bogo	NH	Female	740	1.80	0.16	Ert (AM;1432)
Pari	NH	Female	974	1.20	0.13	Gov (AM;1195)
Mooi	BD	Female	1001	2.14	0.15	Che (AM;1008)
Xaix	NH	Female	1344	2.06	0.26	Gov (AM;1198) Ert (AM;1432)
Upps	NH	Female	1903	0.19	0.09	Gov (AM;1050)
Pret	NH	Female	NA	0.27	0.22	Gov (AM;1048)
LSko	NH	Male	787	1.76	0.12	Can (AM;876)
Tor	BD	Male	866	2.51	0.22	Che (AM;995) Ham (AM;815)
Lek	BD	Male	1034	2.71	0.70	Jag (AM;NA) Oku (AM;761) Prin (AF;1527) Art (AM;850)
Neu	BD	Male	1084	3.20	0.16	Ham (AM;857)
Ert	NH	Male	1401	0.68	0.10	Gov (AM;1051)
Average Female				1.17	0.15	
Average Male				1.64	0.23	
TOTAL Average				1.44	0.20	

Please note that focal individuals are sorted by sex and Elo-ratings. Unfortunately, we could not calculate the Elo-rating of Pret as she became an adult during our study period (by giving birth to her first infant) and we did not have enough agonistic interactions to extract an Elo-rating for the day we observed her greeting Gov.

Table A6. List of behaviours used to describe the social role of both individuals involved in a conflict

Social role	Behaviour	Definition
Aggressor	Aggression calls	Low pitch vocalisations, such as chutter and bark (Struhsaker, 1967)
	Attack	Forward motion of the body towards an opponent
	Bite	Grabbing an opponent with the mouth
	Chase	Running after an opponent who is fleeing
	Grab	Holding an opponent with the hand
	Hit	Slapping an opponent with the hand
	Monopolise	Restraining access to other individuals from a valuable resource
	Stare	Popping up the eyelids towards an opponent
	Take place	Displacing an opponent and taking his/her place
Victim	Avoid	Moving head or body away from an aggressor
	Crawl	Bowing down to an aggressor while looking at him/her
	Flee	Running away from an aggressor as he/she is chasing
	Jump aside	Jumping on the side to avoid an aggressor
	Retreat	Moving without running away from an aggressor

Table A7. Number of males, male-male dyads and observed greetings in the four study groups

Group	N adult males	N male-male dyads	N male-male dyads observed greetings	N greeting calls produced
AK	4	6	2	7 (4)
BD	9	36	12	21 (18)
KB	4	6	5	39 (20)
NH	5	10	6	12 (11)
Total	22	58	25	79 (53)

Note here that two males migrated from one study group to another one during the study period and were counted twice in the total number of adult males as they participated in encounters in both groups. Numbers in parentheses in the last column represent the number of greetings used for the function analysis after modifications to get a binomial structure, i.e. considered as Yes=1 for an observed greeting as soon as at least one vocal signal was produced within a dyad and No=0 if males from a dyad have never been observed greeting.

Table A8. Presentation of the nine steps needed to obtain the restructured dataset

1. Select participating males	We considered every male present in a studied group at least one day during the study period in the analysis
2. Create dyads	We created all the possible male-male dyads (e.g. if group size is four males, then there are six possible dyads, see Table A7)
3. Assign caller/receiver	We represented each dyad twice, with caller/receiver roles reversed
4. Add predictive variables	We added the following three predictors: - Close to rivers = whether greetings occurred <100m of riverbed (Yes/No) - Caller approached = whether the caller was initiating the encounter by actively approaching another male or not (Yes/No) - Feeding involved = whether at least one of the participant was feeding (Yes/No)
5. Take only co-residents male	We excluded all self-dyads (composed by the same male as being the caller and receiver as that was not possible) as well as all dyads composed by males that were not co-residents in one group during the study period
6. Add Elo-rating difference	We obtained a rank difference for a specific dyad by subtracting the average Elo-rating of the receiver of the study period from the one of the caller. Negative values thus mean callers are lower-rated than receivers whereas positive values indicate that callers are higher-rated than receivers
7. Add social bond strength (DSI)	We added the Dyadic Composite Social Index (Silk et al., 2013) for a special dyad by looking at the time two individuals spend grooming, in close proximity (<10m), or as nearest neighbours of each other using focal data
8. Exclude unhabituated subjects	We excluded all the males considered as not well-habituated based on their tenure in the group, on their presence in another studied group before their migration in their current group and the number of days they have been seen in the group during the study period to avoid habituation bias as bold individuals might be observed more frequently than shyer ones
9. Add response variable	We added whether a grunt between two adult males has actually ever been observed at least once or not (Yes=1/No=0) under the conditions specified by the different combinations of outcomes of our predictor variables to examine the functions of greeting signals (see table A9 for further illustration).

1151 Table A9. Example of restructured data set used for the function analysis

Caller	Receiver	Close to rivers	Caller approached	Feeding involved	Cores	Elo-rating difference	DSI	Observed greeting
Art	Lek	No	No	No	67	-223	5.140	0
Art	Lek	No	No	Yes	67	-223	5.140	0
Art	Lek	No	Yes	No	67	-223	5.140	1
Art	Lek	No	Yes	Yes	67	-223	5.140	0
Art	Lek	Yes	No	No	67	-223	5.140	0
Art	Lek	Yes	No	Yes	67	-223	5.140	0
Art	Lek	Yes	Yes	No	67	-223	5.140	0
Art	Lek	Yes	Yes	Yes	67	-223	5.140	0
Lek	Art	No	No	No	67	223	5.140	0
Lek	Art	No	No	Yes	67	223	5.140	1
Lek	Art	No	Yes	No	67	223	5.140	0
Lek	Art	No	Yes	Yes	67	223	5.140	1
Lek	Art	Yes	No	No	67	223	5.140	1
Lek	Art	Yes	No	Yes	67	223	5.140	1
Lek	Art	Yes	Yes	No	67	223	5.140	0
Lek	Art	Yes	Yes	Yes	67	223	5.140	1

Table A10. Results of the GLMM testing the Benign Intent Hypothesis

	Estimate	SE	*Z*	CI *
Intercept	-3.24	0.73	-4.44	-4.67 to -1.81
Presence of food (Yes)	0.34	0.41	0.82	-0.47 to 1.15
Initiator calling (Yes)	-1.47	0.56	-2.61	-2.58 to -0.37
Interaction *Presence of food (Yes) : Initiator calling (Yes)*	-0.56	0.78	-0.71	-2.10 to 0.98

* CI = 95% confidence intervals using Wald method, test levels of categorical predictor are given in parentheses.

Table A11. Results of the GLMM testing the Conflict Management Hypothesis

	Estimate	SE	*Z*	CI *
Intercept	-3.72	0.62	-5.96	-4.94 to -2.50
Rank difference	-0.58	0.33	- 1.75	-1.22 to 0.07
Rank difference (quadratic)	0.19	0.19	0.99	-0.19 to 0.57
Social bond strength (DSI)	0.49	0.35	1.41	-0.19 to 1.17
Presence of food (Yes)	0.17	0.34	0.50	-0.49 to 0.83

* CI = 95% confidence intervals using Wald method, test levels of categorical predictor are given in parentheses.

Table A12. Results of the GLMM testing the Signal Submission Hypothesis

	Estimate	SE	*Z*	CI *
Intercept	-3.62	0.63	-5.72	-4.86 to -2.38
Rank difference	-0.63	0.37	-1.71	-1.36 to 0.09
Presence of food (Yes)	0.17	0.34	0.50	-0.49 to 0.83

* CI = 95% confidence intervals using Wald method, test levels of categorical predictor are given in parentheses.

Table A13. Results of the GLMM testing the Social Coordination Hypothesis

	Estimate	SE	*Z*	CI *
Intercept	-3.99	0.65	-6.17	-5.26 to -2.72
Rank difference	-0.91	0.45	-2.00	-1.80 to -0.02
Social bond strength (DSI)	0.82	0.56	1.48	-0.27 to 1.92
Presence of food (Yes)	0.47	0.39	1.22	-0.29 to 1.23
Close to rivers (Yes)	0.47	0.37	1.27	-0.25 to 1.20
Interaction *Rank difference : Social bond strength*	0.27	0.36	0.74	-0.44 to 0.98
Interaction *Rank difference : Presence of food (Yes)*	0.64	0.33	1.91	-0.02 to 1.29
Interaction *Rank difference : Close to rivers (Yes)*	-0.10	0.32	-0.31	-0.72 to 0.52
Interaction *Social bond strength : Presence of food (Yes)*	-0.27	0.49	-0.55	-1.24 to 0.70
Interaction *Friendship : Close to rivers (Yes)*	-0.13	0.48	-0.27	-1.08 to 0.82

* CI = 95% confidence intervals using Wald method, test levels of categorical predictor are given in parentheses.

Table A14. Results of the GLMM testing the Social Bond Testing Hypothesis

	Estimate	SE	*Z*	CI *
Intercept	-3.52	0.61	-5.73	-4.73 to -2.32
Social bond strength (DSI)	0.55	0.35	1.58	-0.13 to 1.24
Presence of food (Yes)	0.17	0.33	0.50	-0.49 to 0.82

* CI = 95% confidence intervals using Wald method, test levels of categorical predictor are given in parentheses.

Table A15. Results of the GLMM testing the Risk Reduction Hypothesis

	Estimate	SE	*Z*	CI *
Intercept	-3.28	0.69	-4.75	-4.63 to -1.93
Social bond strength	0.59	0.38	1.57	-0.15 to 1.34
Initiator calling (Yes)	-1.77	0.42	-4.18	-2.60 to -0.94
Close to rivers (Yes)	0.56	0.36	1.56	-0.14 to 1.26

* CI = 95% confidence intervals using Wald method, test levels of categorical predictor are given in parentheses.

FIGURES CAPTION

Fig 1. Map showing the location of dyadic encounters collected during focal follows according to groups (orange = BD, yellow = IN, dark violet = NH) and whether a grunt was produced (vocal encounters in black and silent ones in colours). The blue polygon represents the variable close to rivers, i.e. areas within 100m of riverbed. *Source:* “Mawana” 28°00'25.07" S and 31°11'47.07" E. **Google Earth**, version 7.1.5.1557, 8 July 2016, available at https://www.google.com/earth/.

Fig 2. Effect of the sex of partner on grunt production by focal. Shown are model estimates with associated 95% confidence intervals.

Fig A1. Map showing the location of predator encounters (yellow = terrestrial mammal, green = snake, pink = eagle) according to their distance from rivers (i.e. considered as near rivers when points are in the blue polygon representing 100m from the riverbed). *Source:* “Mawana” 27°59'41.89" S and 31°10'14.26" E. **Google Earth**, version 7.1.5.1557, 8 February 2014, available at https://www.google.com/earth/.

Fig A2. Mosaic plot of predator type encounters according to proximity to rivers (Yes when close to rivers, No otherwise). The red line represents the distribution of predators encounters randomly distributed across rivers.

Fig A3. Elo-ratings of focal animals from NH group over the entire study period (5AF: Bogo, Pari, Pret, Upps, Xaix & 4AM: Can, Ert, Gov, LSk). An initial rating of 1000 was assigned to immigrant males and adult females (after given birth for the first time). Note that we can see the evolution of Elo-ratings through time according to single agonistic interactions: the ratings of winners increase while the ratings of losers decrease.

Fig A4. Spectrogram of three grunts produced during an encounter between two adult males

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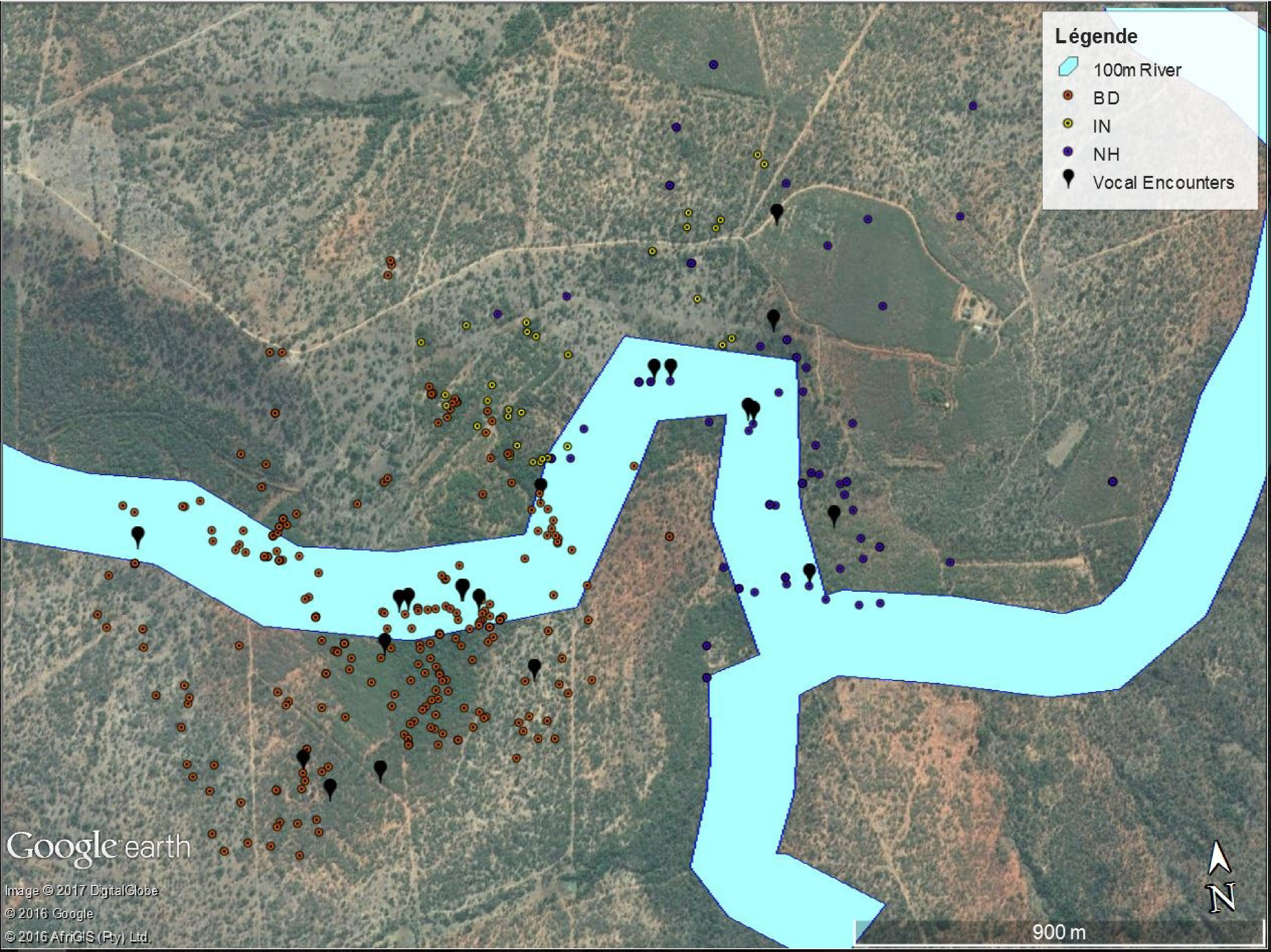
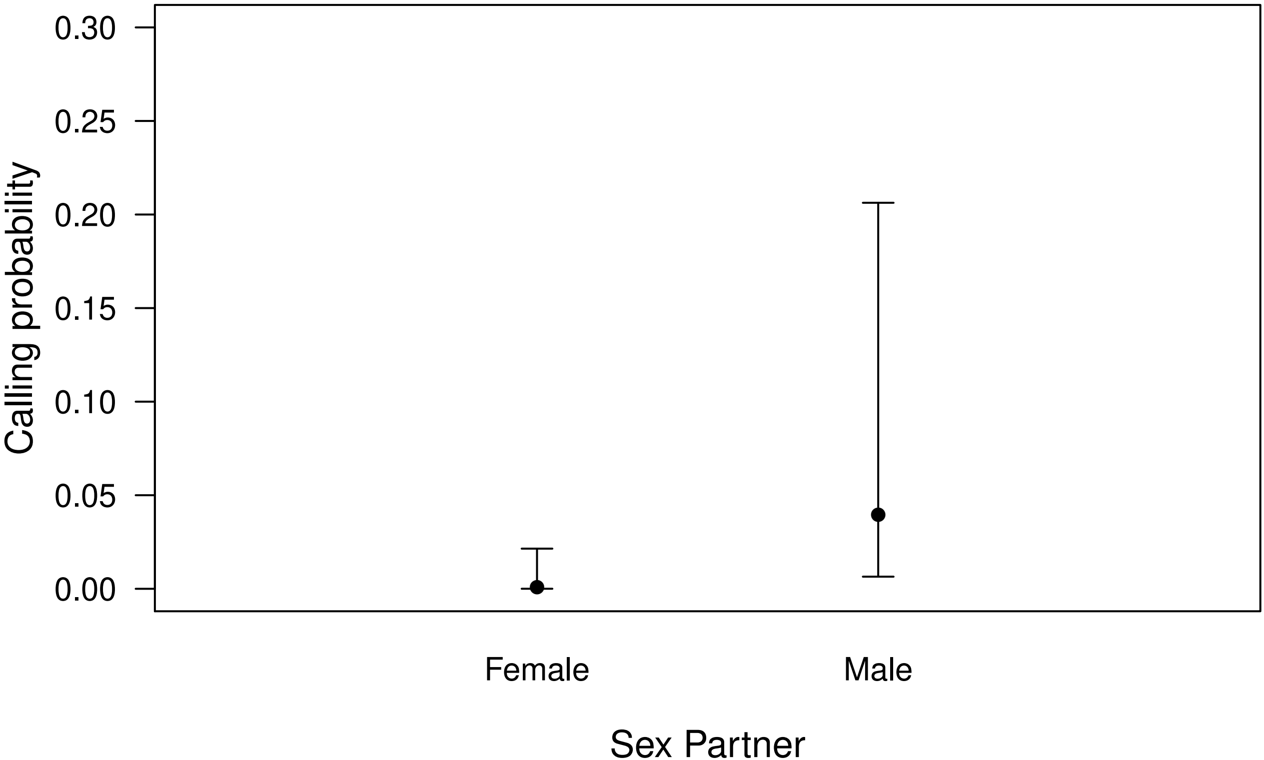


Légende
100m River
BD
IN
NH
Vocal Encounters
Google earth
Image © 2017 DigitalGlobe
© 2016 Google
© 2016 AfriGIS (Pty) Ltd.
900 m
N



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0.25
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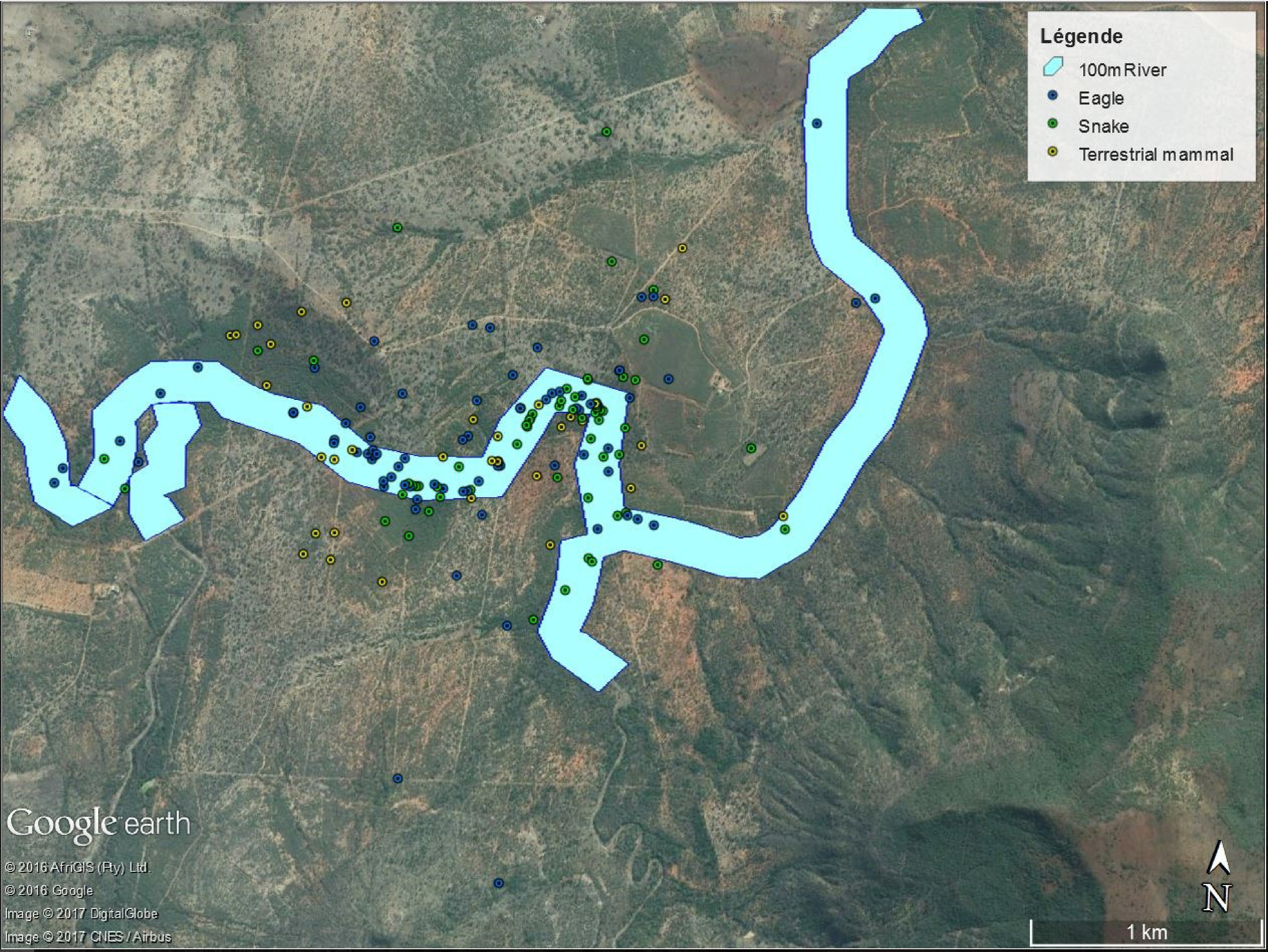
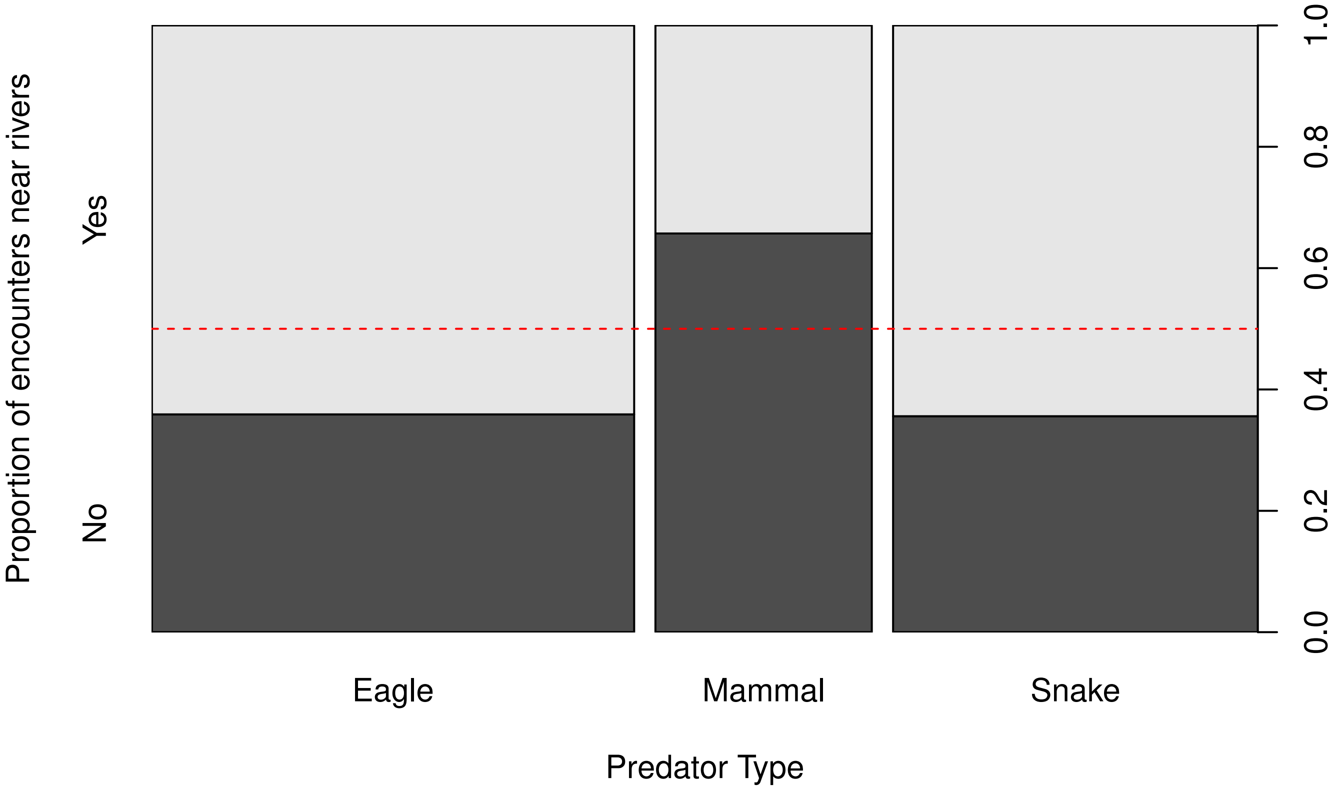
0.15
0.10
0.05
0.00
Calling probability
Female
Male
Sex Partner


Légende
100m River
Eagle
Snake
Terrestrial mammal
Google earth
© 2016 AfriGIS (Pty) Ltd.
© 2016 Google
Image © 2017 DigitalGlobe
Image © 2017 CNES / Airbus
N
1 km



Proportion of encounters near rivers
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No
Eagle
Mammal
Snake
Predator Type
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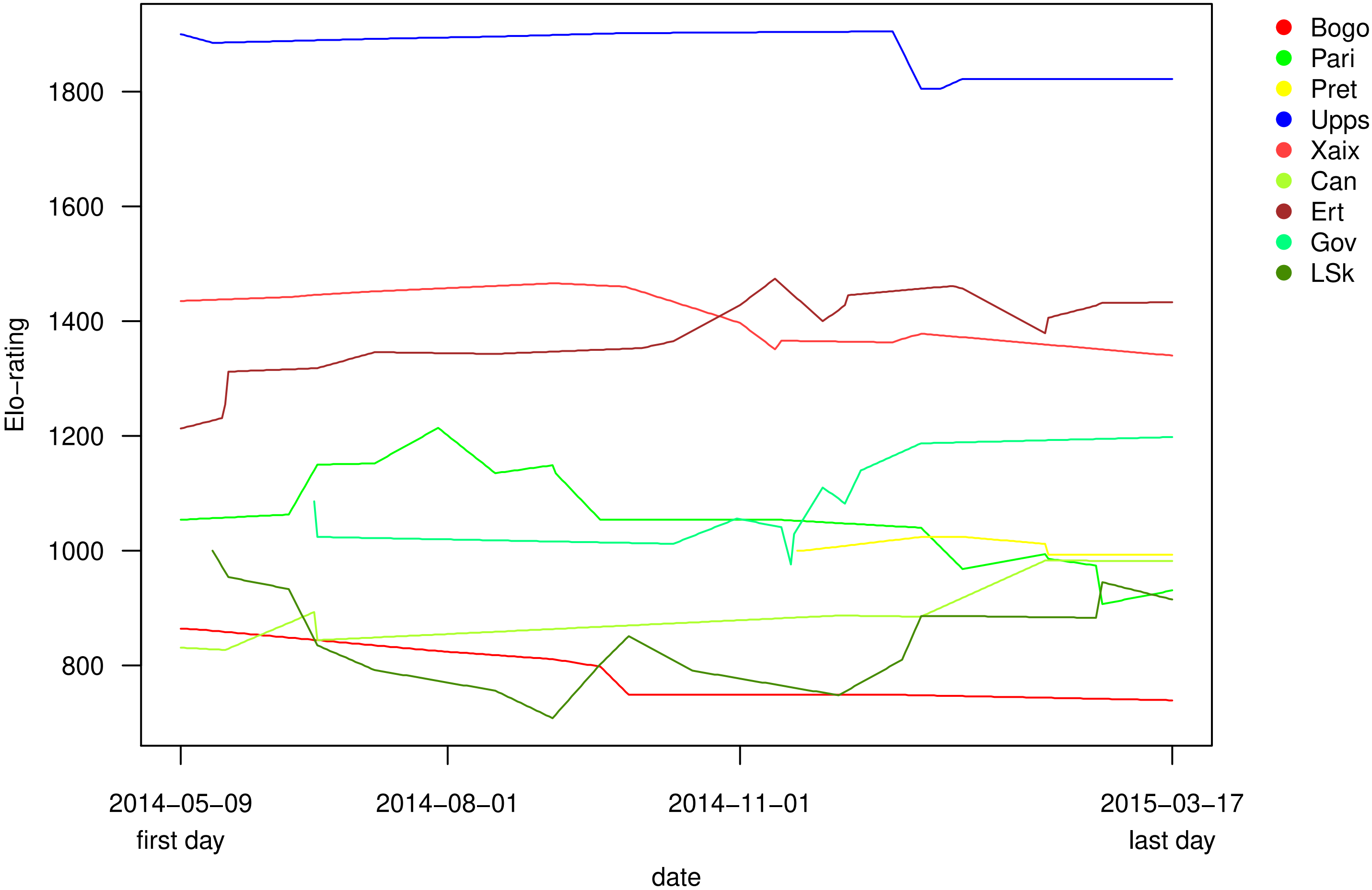
0.2
0.4
0.6
0.8
1.0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Pret
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Can
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Gov
LSk
Elo−rating
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1000
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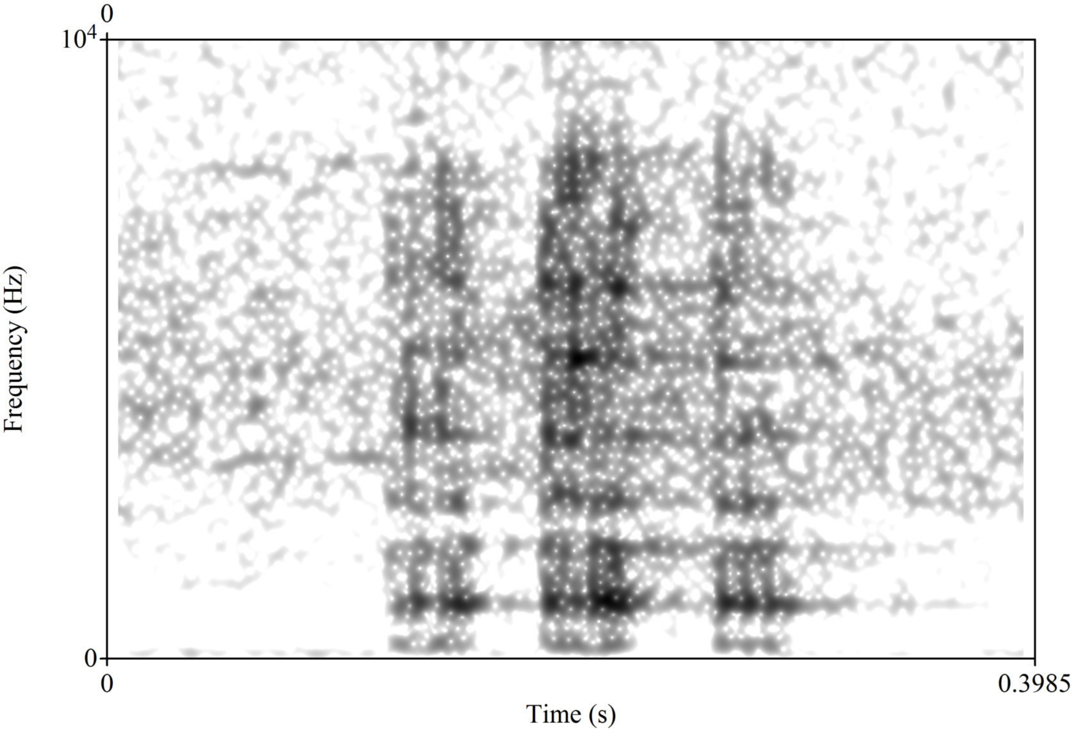
last day
date



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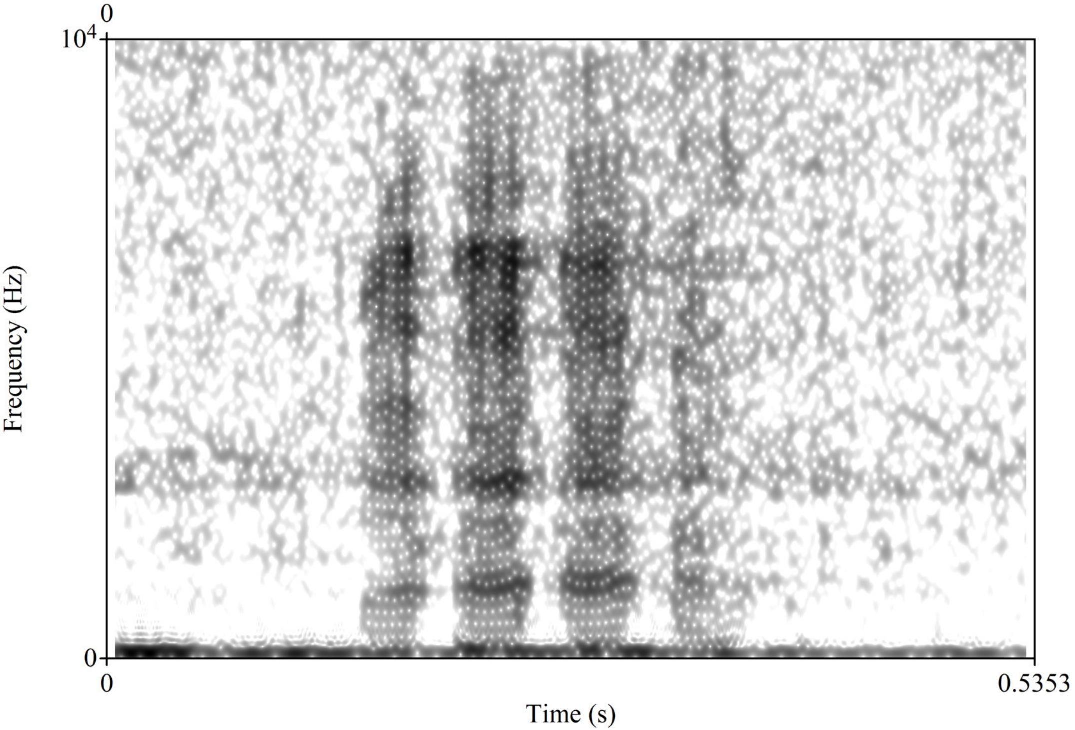
Time (s)



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